Optimal monitoring and statistical modelling methods for feral cats and other mammalian predators in a pastoral landscape

---

A thesis by manuscript
submitted in partial fulfilment
of the requirements for the Degree of
Doctor of Philosophy

at
Lincoln University
by
Margaret Nichols

Lincoln University
2018

Thesis by Manuscript

This thesis by manuscript is built around a set of peer-reviewed published manuscripts and manuscripts prepared for submission.

Optimal monitoring and statistical modelling methods for feral cats and other mammalian predators in a pastoral landscape

by

Margaret Nichols

Abstract

Introduction. Mammalian predators have a global impact on biodiversity. Mammalian predator species often occur at low abundance and require efficient and non-invasive monitoring techniques, alongside reliable statistical modelling methods, to explain the probability of detection, presence and, when possible, abundance. Camera traps are a dynamic technology currently used around the world to monitor a wide range of species in a variety of ecological research programmes However, as camera traps continue to change and improve, there is a need for more standardisation for both camera settings and deployment methods, depending on the objective of the study.

Aims. The aims of this study were to: 1) determine the optimal orientation for camera traps to detect mammalian pest species; 2) determine the optimal statistical method for modelling changes in a feral cat population pre-and post-predator control operation; 3) assess the effectiveness of a Bayesian abundance estimator at providing abundance estimates for a population of hedgehogs pre- and post-predator control; and 4) deploy camera traps on a wide scale to determine the baseline relative abundance and detection rate for feral cats prior to a predator control operation.

Materials and methods. 1) I deployed 20 pairs of camera traps (one horizontal and one vertical) for 21 days across a pastoral landscape in Hawke's Bay, North Island, New Zealand, and compared numbers of detections for target species (feral cats) and mustelids (*M. furo, M. erminea, and M. nivalis*); 2) I deployed 40 horizontally-oriented cameras on pre-determined grid sites across two pastoral properties in Hawke's Bay, for two consecutive periods of 21 days, to monitor feral cats pre- and post-predator control. I compared four statistical modelling methods for gauging the success of the control operation: index manipulation

method (IMI), capture-mark-recapture (CMR), a generalised linear mixed model method (GLMM), and the spatial presence-absence model (SPA). The IMI method was used as a benchmark method for comparison as used in previous studies; 3) I used the same camera trap data from the previous/an earlier?? chapter to estimate hedgehog abundance pre- and post-control, using the SPA model; and 4) I deployed 68 horizontally-oriented cameras on a wide scale (26,000 ha) across two pastoral areas of coastal Hawke's Bay (*The Cape to City* restoration project) for 21 days, to monitor feral cats prior to a predator control operation. I compared the GLMM method from the previous study with an abundance-induced heterogeneity model (RN) for estimating the proportion of cameras detecting cats per site and the relative abundance at each site. I also used the RN model to compare the effect of habitat type (forest, forest margin, mixed, and open) on the abundance and proportion of detections.

Results. 1) Horizontal cameras produced a significantly greater number of photos overall ($P < 0.001$) and more independent encounters with the target species ($P = 0.03$). Orientation did not influence the number of false triggers ($P = 0.53$); 2) The IMI and SPA models gave similar, accurate estimates showing a decrease in cat abundance (90% and 88%, respectively) post-predator removal. The GLMM method showed a significant decrease in camera detection rates post-control (90%). The CMR models were unable to give accurate abundance estimates due to the low sample size of reliably identifiable cats; 3) The SPA model produced more precise estimates for a population of hedgehogs (due to a higher number of multiple detections than feral cats) and successfully showed a reduction in abundance post-predator control; 4) Strategically placed cameras had much higher detection rates than previous studies with the GLMM method estimating 5.2% (95 % C.I 2.3-7.9) for Site 1, and 4.3% (2.6-10.3) for Site 2. The RN model estimated detection rates of 5.5% (95% CI 4.1-6.9) for Site 1, and 4.5% (3.1-5.9) for Site 2. The RN model also indicated variation in the relative abundance based on habitat type with significantly higher detection rates in forests and along forest margins compared with mixed scrub and open farmland.

Discussion and conclusions. Horizontally-oriented cameras performed well at detecting feral cats and mustelids. While the GLMM method and the SPA model gave accurate results in comparison to the IMI method, they lacked precision. CMR models have had success with large, well marked felids;, however, they do not perform well with a small sample size of identifiable cat images (very few clearly marked individuals). Although requiring two separate measures (pre-monitoring, manipulation, then post-monitoring), the IMI method was simple to calculate using a variance equation and appeared to be accurate. This may be a valuable method for implementation by wildlife managers in the future.

The SPA model performed well (more precision) for hedgehogs, for which there were more multiple detections per camera station. This model requires large amounts of data and is more appropriately suited for a species that occurs at higher densities than feral cats. However, a further examination of the size of hedgehog home ranges and the possibility that they simply saturated the detection network with high numbers, must be done to ensure that the model's requirement for spatially-correlated detection units has been satisfied.

Both the GLMM and RN model showed no substantial differences in cat detections for either site prior to a predator control operation. The RN model was able to incorporate heterogeneity at the individual camera station level; thus, it provided more precise estimates at the overall site level.

Keywords: Camera traps, invasive species, predators, wildlife management, detection, abundance

Manuscripts prepared and submitted arising from this Thesis and statement of authors' contribution

A comparison of horizontal versus vertical camera placement to detect feral cats and mustelids

SHORT-COMMUNICATION

(Appendix A)

Margaret Nichols[1], Alistair S. Glen[2], Patrick Garvey[3] and James Ross[1]*

[1]Centre for Wildlife Management and Conservation, Lincoln University, Canterbury, New Zealand

[2]Landcare Research, Private Bag 92170, Auckland 1142, New Zealand

[3]School of Biological Science, Tamaki campus, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand

MN planned and carried out field trials, analysed and interpreted data, and wrote the manuscript. AG helped with experimental design, and manuscript preparation, PG assisted with field trial set-up. JR gave statistical advice and commented on the manuscript.

Manuscript accepted 1st September 2016, and published online early 30th September 2016. New Zealand Journal of Ecology 41(11): 145-150

Exploiting interspecific olfactory communication to monitor predators

(Appendix B)

Patrick M. Garvey [1,2], Alistair S. Glen [2], Mick N. Clout [1], Sarah V. Wise [1,3], Margaret Nichols, [4] Roger P. Pech [5]

[1] Centre for Biodiversity and Biosecurity, School of Biological Sciences, University of Auckland, Auckland, New Zealand

[2] Landcare Research, Private Bag 92170, Auckland, 1142 New Zealand

[3] Royal Botanic Gardens Kew, Wakehurst Place, RH17 6TN United Kingdom

[4] Centre for Wildlife Management and Conservation, Lincoln University, Canterbury, New Zealand

[5] Landcare Research, PO Box 69040, Lincoln, 7640 New Zealand

PG planned and carried out field trials, analysed and interpreted data, and wrote the manuscript. AG, MC, and RP helped manuscript preparation. SW helped with analysis, and MN assisted with field trials and data collection.
Manuscript published online in *Ecological Applications* 1st February 2017, 27(2).

Wildlife detector dogs and camera traps: a comparison of techniques for detecting feral cats
(Appendix C)

AS Glen [a], D Anderson [b], CJ Veltman [c], PM Garvey [d] & M Nichols [e]
[a] Landcare Research, Auckland, New Zealand
[b] Landcare Research, Lincoln, New Zealand
[c] Department of Conservation, c/o Landcare Research, Palmerston North, New Zealand;
[d] Centre for Biodiversity and Biosecurity, School of Biological Sciences, University of Auckland, New Zealand
[e] Centre for Wildlife Management and Conservation, Lincoln University, Canterbury, New Zealand

AG, DA, and CV designed and carried out field trials, as well as manuscript preparation. PG and MN carried out field trials and data collection.

Manuscripts currently submitted to journals

A Comparison of statistical modelling methods for evaluating the effectiveness of a feral cat control operation using camera traps

Margaret Nichols[1], Alistair S. Glen[2], James Ross[1], Patrick M. Garvey[2]

[1]Centre for Wildlife Management and Conservation, Lincoln University, Canterbury, New Zealand

[2]Landcare Research, Private Bag 92170, Auckland, New Zealand 1142

MN planned and carried out field trials, analysed and interpreted data, and wrote the manuscript. AG assisted with experimental design and commented on the manuscript, JR helped prepare the manuscript and statistical analyses, PG assisted with field trial set-up.

Manuscript submitted for publication in *Wildlife Research* 27th April 2017

An evaluation of strategically and widely-spaced camera traps for monitoring feral cats (*Felis catus*) in NZ

Margaret Nichols[1], James Ross[1], Alistair S. Glen[2], Adrian Paterson[1]

[1]Department of Pest-management and Conservation, Lincoln University, Canterbury, New Zealand

[2]Landcare Research, Private Bag 92170, Auckland, New Zealand 1142

MN planned and carried out field trials, analysed and interpreted data, and wrote the Manuscript. JR helped manuscript preparation and statistical analyses, AG assisted with experimental design and commented on the manuscript. AP assisted with manuscript preparation.

Manuscript submitted for publication in *Austral Ecology* 26th June 2017

Using a spatially explicit presence-absence model to measure hedgehog (*Erinaceus europaeus*) abundance

(In preparation for submission)

Margaret Nichols[1], James Ross, Adrian Paterson[1], Alistair S. Glen[2], Patrick M. Garvey[2]

[1]Centre for Wildlife Management and Conservation, Lincoln University, Canterbury, New Zealand

[2]Landcare Research, Private Bag 92170, Auckland, New Zealand 1142

MN planned and carried out field trials, analysed and interpreted data, and wrote the manuscript. JR assisted with experimental design and statistical analysis. AP assisted with manuscript preparation. AG assisted with experimental design. PG assisted with field trial set-up and manuscript preparation.

Manuscript to be submitted to *Wildlife Biology* May 2018.

Acknowledgements

I would like to thank the following people who contributed and gave support throughout my PhD research.

My supervisors, James Ross, Al Glen and Adrian Paterson, for their advice, guidance, statistical prowess and overall positive outlook. I have been incredibly lucky not only for their true expertise in the field of wildlife management, but also for their role modelling as well balanced and successful researchers. I have become a genuinely better person from their influence. On the same note, I would also like to thank Elaine Murphy for her role modelling as a highly successful researcher in this field, as her endless positivity added to my enjoyment of this subject material. Thanks to Patrick Garvey for your endless humour and great knowledge both in and out of the field as we both completed trials towards our PhDs.

I would also like to thank the entire ZIP (Zero Invasive Predators) team for patiently supporting me while I finished this thesis.

This research was funded by the Hawke's Bay Regional Council and by core funding from the Ministry of Business, Innovation and Employment.

Thanks to Andrew Gormley of Landcare Research and Andrew Bengsen of NSW Department of Primary Industries for their statistical analysis contribution of both time and materials. Thanks to Rod Dickson and Campbell Leckie of the Hawke's Bay Regional Council for their dedicated support of the field trials and the acquisition of funding. Thanks also to Sam Cave for his fieldwork expertise and guidance through the back country terrain.

Finally, huge thanks goes to my family and friends who have been nothing less than supportive and delightful throughout this process. I would especially like to thank my sister, Liz, who has trudged through all this before me, and who always shared great wisdom with me about writing and research but, most importantly, finding the treasured balance we all seek to live a fulfilled and purposeful life.

Table of Contents

List of Tables

List of Figures

List of Abbreviations

AIC	Aikaike Information Criterion
CI	Confidence interval
CMR	Capture-mark-recapture
Df	Degrees of freedom
GLM	Generalised linear model
GLMM	Generalised linear mixed model
g_0	Probability of detection at the centre of an animal's home range
IMI	Index-Manipulation-Index
IR	infrared
MBI	Ministry of Business, innovation, and employment
NSW	New South Wales
PAPP	*Para*-aminopropiophenone
SPA	Spatial-Presence-Absence
σ	Rate at which detection probability declines with increasing distance from the centre of an animal's home range

Chapter 1

Introduction

1.1 Background

Island ecosystems often have a variety of native and endemic species that are easily disrupted by the introduction of invasive mammalian species, typically through predation, disease and competition for resources (Domigan & Hughey 2008; Tompkins et al. 2013; Medina et al. 2014). The combination of global climate change and the continuing invasion of alien species brings about an even greater threat to these systems (Nogales et al. 2004; Tompkins et al. 2013; Oppel et al. 2014). The management and restoration of native flora and fauna often requires monitoring and removal of invasive species, especially when those invasive species constantly reinvade, such as feral cats (*Felis catus*), mustelids (*Mustela furo, M. nivalis, and M. erminea*) and hedgehogs (*Erinaceus europaeus*) (Alterio et al. 1998; King 2005; King et al. 2007; Medina et al. 2014; Oppel et al. 2014).

Accurately assessing the presence and abundance of pest species is fundamental to better management of pest species that both reinvade predator-free island ecosystems and those that persist in mainland areas (Alterio et al. 1998; Nogales et al. 2013). Efficient monitoring of invasive species is vital to the success of control operations (Alterio et al. 1998; Chapman & Balme 2010; Bengsen et al. 2012). Wildlife managers now realise that non-invasive monitoring methods suitable for wide scale monitoring programmes are necessary to understand the presence and abundance of these species (Pollock et al. 2002; Gompper et al. 2006; Sweetapple & Nugent 2011).

Carnivores are particularly elusive to monitor, and require a variety of techniques to manage efficiently (Alterio et al. 1998; Gompper et al. 2006; Long et al. 2007b; Kelly & Holub 2008; Wang & Macdonald 2009; Chapman & Balme 2010; Glen et al. 2013). Complete direct counts of a population are often too expensive to justify and difficult because of large sampling areas (Edwards et al. 2000; Ball et al. 2005). Accordingly, making inferences into the relative abundance of a species, by sampling subsets of the population, becomes vital for monitoring in an area (Edwards et al. 2000; Pickerell et al. 2014). Over time, a variety of direct and indirect monitoring methods have been used to monitor different pest species (Russell et al. 2012; Lazenby et al. 2015a). These techniques include spotlight counts, tracking tunnels/plots, track pads, camera traps, hair snags, live capture and

surveys (including scat detection dogs and DNA markers) (Alterio et al. 1998; Edwards et al. 2000; Gompper et al. 2006; Long et al. 2007b; Russell et al. 2012; Lazenby et al. 2015a). Caution must be taken when using direct and indirect monitoring methods (in particular spotlight counts and tracking plots) with wild felids, as they often significantly underestimate populations due to their elusive behaviour and low densities (Jackson et al. 2006; Letnic et al. 2011; Guthlin et al. 2014; Lazenby et al. 2015a). DNA samples, either through scat detection, hair snags or, even, live trapping, are expensive to obtain and so may not be a viable option for many monitoring operations (Glen et al. 2016). Although there are a variety of monitoring methods available, decisions for their use should be based on a variety of factors, such as target species (morphology and behaviour), habitat, season and study objective (Guthlin et al. 2014). Large tracking tunnels designed for cats have had some success (Pickerell et al. 2014). In Pickerell et al. (2014), tracking tunnels had a much greater efficiency at detecting cats than kill traps, such as the Conibear; however, when cats occurred at low densities, neither methods were as effective at detecting cats.

Thesis structure

Chapter 1 provides a brief introduction to the subject of optimal deployment strategies for camera trapping predators such as feral cats, mustelids and hedgehogs.

In Chapter 2, I provide and in-depth literature review pertaining/about?? To feral cats as a target species, other predators such as hedghogs and mustelids, briefly, as target spieces, and also the available monitoring methods and statistical modelling methods.

In Chapter 3, I investigate which orientation of a camera trap, horizontal or vertical, detects the highest number of target species (feral cats and mustelids).

In Chapter 4, I invesigate how four different statistical models (IMI, CR, GLMM, SPA) compare at measuring the success of an intensive predator control operation targeting feral cats.

In Chapter 5, I estimate hedgehog abundance and detection probability with the SPA model from Chapter 4. I investigate whether the model converges with greater precision when used on a species that occurs naturally at a higher density.

In Chapter 6, I investigate camera trapping strategies at the macro-scale (i.e. the *Cape to City* restoration project in Hawke's Bay), and whether strategic placement towards good predator habitat increases detections. I also compared the RN model with the GLMM method previously implemented to model detection rates at the two sites. I also examine if detection rates vary by habitat type, using the RN model.

Finally, in Chapter 7, I summarise results and discuss the implications of these results from each chapter study.

Chapter 2 Literature Review

2.1 A brief history of domestic house cats as an introduced species

In the mid 1700s, European explorers brought domestic cats (*Felis catus*) to New Zealand and various offshore islands (Gillies 2005). By 1900, a large, self-sustaining feral population was clearly established (Long 2003; Algar & Brazell 2008; Eason et al. 2010). Cats have fully dispersed through the three main islands of New Zealand and are found on 31 of its offshore islands (Gillies & Fitzgerald 2005). Ships often brought with them many rodent pests, and cats were useful for vermin control on long journeys (Gillies & Fitzgerald 2005). Cats were noted for the destruction of many indigenous species in the Hutt Valley, as early as in 1840 (Gillies & Fitzgerald 2005). The occasional killing of cats began in 1860 when they were considered to be very numerous. However, as rabbit numbers rose out of control, cats were eventually re-distributed through farmland for biological control (Gillies & Fitzgerald 2005).

Since their introduction, cats have been eradicated from six New Zealand offshore islands and naturally died out on three (Long 2003). Although the majority of people are aware of feral cats as a conservation issue, many places around the world still view them as necessary for vermin control (Abu-Madi & Behnke 2014). Feral domestic cats have become a major threat to wildlife in New Zealand and abroad (Forin-Wiart et al. 2014; Burton et al. 2015). There are three different grades of cats, ranging from purely domestic to self-sufficient: 1) house cats living with humans who provide them with all the necessary resources; 2) stray cats that are loosely dependent on humans; and 3) feral cats that are totally self-sufficient (Forin-Wiart et al. 2014; Medina et al. 2014). Feral cats are often differentiated from domestic cats as living away from human contact and being totally self-sufficient in aquiring resources (Forin-Wiart et al. 2014; Medina et al. 2014; Fisher et al. 2015). These medium-sized predators adapt quickly to their environments, making them successful at colonising new areas (Abu-Madi & Behnke 2014; Allen et al. 2015).

2.1.1 Feral cat morphology, behaviour, and diet

Feral cats, on average, weigh 1-5 kg (Gillies & Fitzgerald 2005) and are 535-885 mm in length (including the tail) (Long 2003). Cats have a distinctive dental arrangement, made up

mostly of canines for severing the necks of prey, and carnassials for trimming soft tissue from the bones (Bradshaw 2006). Cats can be identified by five different types of 'tabby' coat patterns (Robley et al., 2010) along with other coat colours, such as ginger, black, grey, or tortoiseshell (Fisher et al. 2015). Cats in more secluded island ecoystems may only represent one or two different coat patterns, due to their reduced gene pool (Gillies & Fitzgerald 2005). Variation in colouration and unique coat patterns allows the possibility of individual identification. Cats have highly perceptive hearing, up to 65 kHz, and exceptional night vision that can detect objects illuminated by 1/6 of that required by humans. However, cats' daytime vision is diminished and they are effectively colour-blind in most daylight conditions (Gillies & Fitzgerald 2005).

Cats are considered obligate carnivores (Bradshaw et al. 1996; Doherty et al. 2015). If necessary, cats may feed on carrion, but their preferred choice is fresh meat (Bradshaw et al. 1996). Feral cats can have a similar diet to domestic house cats but can adapt quickly to the available food resources (Long 2003). Reviews of dietary research by Medina et al. (2014) and Fisher et al. (2015) reported a range of prey species present in feral cats' gut contents, including small mammals, invertebrates, reptiles, fish, amphibians, and birds. Due to the relatively small size of their prey, feral cats eat regularly throughout a 24 h period (Bradshaw et al. 1996; Bradshaw 2006). In New Zealand and Australia, when the cats' preferred prey (European rabbit, *Oryctolagus cuniculus*) are scarce, prey switching can occur, leaving native species exceptionally vulnerable (Murphy et al. 2004; Fisher et al. 2015). There is also a difference between the diets of feral cats on the NZ mainland compared to their diets in island habitats. Feral cats living on the mainland have a wide variety of mammalian prey species to choose from, including rabbits, rodents, brushtail possums (*Trichosurus vulpecula*), hedgehogs and small mustelids (Gillies & Fitzgerald 2005). Generally, cats on islands are relegated to a few invasive mammalian species, such as rabbits and rodents and, as a result, prey more heavily on bird populations (Gillies & Fitzgerald 2005).

Behavioural studies show cats are often motivated to kill by visual and auditory cues, not merely for resource acquisition, leading to even further devastation for many prey species (Bradshaw 2006; Fisher et al. 2015; McGregor et al. 2015). Feral cats hunt and consume multiple meals per day although, even under confined laboratory conditions, cats prefer to take small portions of food over an entire day, making this a behavioural trait unrelated to resource availability (Bradshaw et al. 1996). Cats are solitary hunters (Bradshaw et al. 1996), although females may have overlapping home ranges (Gillies & Fitzgerald 2005). Hunting behaviour may be classified as 'stationary', where a cat waits at a point of interest, such as the entrance of a prey animal's burrow, or 'mobile' where a cat moves around their home-range

in search of available prey (Doherty et al. 2015). However, both methods may be used depending on the habitat and individual preference.

Feral cats have developed methods for dealing with resources that may disadvantage their dietary requirements and/or overall well-being (Bradshaw 2006). To avoid creating a nutrient deficiency, cats have developed what is now known as the 'monotony effect' where they may select against any food source that becomes the majority of their diet (when other options are available) (Bradshaw 2006). Though not yet investigated, there may be a genetic predisposition for some cats towards selected hunting strategies and different prey species (Bradshaw 2006). Current research suggests hunting strategies and prey selection are more likely based on a cat's ability to learn to avoid imbalanced food sources (or toxins) and select more nutrient rich resources (Bradshaw 2006). Diet is an important driver in cat behaviour, but resource selection is predominantly motivated by hunting stimuli (Fisher et al. 2015). Cryptic behaviour in feral cats makes them a difficult target for control operations (Fisher et al. 2015). Avoidance of humans is a common trait among feral cats, especially if feral individuals had rarely seen a human (Fisher et al. 2015). Cats are difficult to approach in their environment and may exhibit behaviours that make them difficult to detect, such as cowering in fear or trying to hide when placed in confined spaces (Fisher et al. 2015). Neophobia towards humans may contribute to the issue of low detection using artificial trapping systems that contain human scent and, possibly, foreign sounds and sights (Fisher et al. 2015).

2.1.2 Feral cat habitat and home range

Feral cats use a range of habitats, from pastoral landscapes, to glacial valleys, grasslands, woodlands and, even, deserts (Doherty et al. 2015). Feral cats' activity is driven by a number of factors, including resource availability (prey and shelter), competition, and/or predation, and human influence (Doherty et al. 2015). Cats can be found in most terrestrial habitats throughout New Zealand, from sea level up to 3000 m, spanning sand dunes to grasslands, and exotic and native forest (Langham & Porter 1991; Gillies & Fitzgerald 2005).

Recio et al. (2015) described a preference for densely vegetated habitats as shelter (Edwards et al. 2001) and open grassland for long distance movement. Feral cats often prefer well-covered areas, such as woodlands, hollow stumps, rock piles, bushes, and water features. There are a number of questions still surrounding the way in which cats use different habitats for their survival advantage (McGregor et al. 2015). Cats use surrounding patches of vegetation cover to stalk prey, then open areas for the final ambush (McGregor et al. 2015). McGregor et al. (2015) examined feral cat behaviour through animal-borne video systems (attached to collars), to assess variable behaviours through a dynamic landscape. Their results

were conclusive in showing cats to be 4.1 times more successful at predation in open habitats than complex, vegetated areas. Cats are 70% more likely to have a successful kill in an open area (McGregor et al. 2015). Conversely, feral cats are generally shown to prefer dwelling in complex habitats, such as rocks and dense vegetation (Doherty et al. 2015).

An in-depth understanding of feral cat home-range size is necessary to manage their impact across various landscapes (Abbott 2002). While male feral cats often use the distribution of females to determine their home-ranges, female cats are more dependent on resource availability and the distribution of other females (Abbott 2002). Therefore, in highly productive resource areas (high prey abundance), female cats have smaller home-ranges than males (Edwards et al. 2001; Abbott 2002; Gillies 2005). There is great variation in documented home range sizes (Bengsen et al. 2012), from ~1 km^2 in New Zealand pastoral locations (Langham & Porter 1991), to up to 20 km^2 in Australia's arid regions, as well as various parts of the Northern hemisphere, e.g. Scotland and the Galapagos Islands (Biró et al. 2004). Seasonal variations in prey must be considered as this can increase the home range size (Edwards et al. 2001; Abbott 2002). For instance, feral cats in the grasslands of the South Island, New Zealand tend to have larger home-ranges due to the shortage of prey resources (Moller & Alterio 1999). Recio et al. (2015) used enhanced GPS tracking devices to explore the relationship between home-range size of feral cats and rabbit distribution near braided river corridors in South Island, New Zealand. They found cat movements to be highly correlated with rabbit presence, but also with the least energy cost (e.g. moving close to tracks and roads when travelling longer distances).

There are very few density estimates of feral cats in New Zealand (Gillies & Fitzgerald 2005). However, as in most species, they are resource dependent, and so can be extremely varible (1 to 30/km^2 cats (Gillies & Fitzgerald 2005). In Stewart Island, during low prey densities, feral cats were found at approximately 0.19 to 0.27/km^2 (Harper 2002). In a similar landscape to the field sites in this thesis, Hawke's bay farmland was reported to have a density of 3 to 5.6/km^2 cats (Langham & Porter 1991).

2.1.3 Feral cat impact: predation and beyond

Feral cats are responsible for an estimated 14% of the global mammal, reptile, and bird extinctions (Medina et al. 2011; Nogales et al. 2013; Medina et al. 2014). Many island species are unaccustomed to mammalian predators and, so, must adapt to identify a predation risk (Medina et al. 2014; Robley et al. 2014). Although predation is a significant factor in species decline, indirect effects, such as spread of disease and change in prey behaviour, are also threats (Medina et al. 2014). Independent of lethal consequences, the presence of predators

has a deleterious effect on many vulnerable prey species in both their behavioural and ecological functions, such as through disease transmission, competition for food resources and habitat (Medina et al. 2014). Declines in reproductive success due to predation stress is an example of an indirect effect of feral cat presence in island ecosystems (Medina et al. 2014). The impact made by cats are often increased by the presence of humans and human-driven destruction of a habitat (Medina et al. 2014). Feral cats are generally regarded as a top predator when colonising most island ecosystems (Nogales et al. 2013). There are numerous examples of the impacts of feral cats on island ecosystems, particularly in the Pacific region (Long 2003). For example, Macquarie Island has seen cats significantly reduce petrel (*Pterodroma lessonii*) abundance (Gillies & Fitzgerald 2005). San Nicolas, an island off the Californian shore, is home to only two native mammals, the island fox (*Urocyon littoralis dickeyi*) and a deer mouse (*Peromyscusmaniculatus exterus*), 13 terrestrial birds, and five sea bird species (Ramsey et al. 2011). San Nicolas has seen significant decline throughout these populations due to feral cat predation (on bird species and the deer mouse) and the spread of disease (*Toxoplasma* sp.) to the sea otter (*Enhydra lutris nereis*) and the island fox (Ramsey et al. 2011).

In New Zeand, various species of skinks (*Cyclodina whitakeri*, *Oligosoma nigriplantare polychroma*, *O. zelandicum*) and geckos (*Hoplodactylus maculatus*) are at high risk of predation by feral cats (Hoare et al. 2007). Some ground nesting species, such as kiwi (*Apterygiformes*) (McLennan et al. 1996) and yellow-eyed penguin (*Megadyptes antipodes*) (Alterio et al. 1998), are also particularly vulnerable to cat predation, and require perennial feral cat control, while other vulnerable bird species (shore-birds in particular) only require seasonal control of cats during breeding times (Fisher et al. 2015).

Feral cats also impact other species by spreading disease; most notably cats are primary carriers of the protozoan parasites, *Toxoplasma gondii* and *Sarcocystis gigantea* which lead to the condition known as toxoplasmosis (Afonso et al. 2006; Afonso et al. 2007). Toxoplasmosis has an impact on reproductive success for many species, including wildlife, humans, and livestock (Dickman 1996; Abu-Madi & Behnke 2014). Both humans and other animals may experience abortions and/or severely compromised growth of a foetus when infected with toxoplasmosis (Afonso et al. 2006). The most common transmission of toxoplasmosis is through oocysts, which are excreted by cats into the soil, and they may remain infectious for up to 18 months (Afonso et al. 2006). Small animals, such as birds and mice, are easily infected with these protozoan parasites, and the life cycle is completed when they area preyed upon by cats (Afonso et al. 2006). Cats carry and spread other pathogens, both bacterial and viral (Bevins et al. 2012). Bevins et al. (2012) examined different

transmission types in domestic cats and other felids, such as environmental exposure, through a vector, and through direct contact. *Bartonella* spp. was found in 45% of domestic/feral cats, while only 1% carried the *Toxoplasma gondii* parasite (Bevins et al. 2012). Results suggested that transmission by direct contact may be more determined by behaviour and encounters with other individuals, while infection by indirect exposure to diseases, such as *Bartonella,* and environmental exposure (infected prey) fluctuates between sites (Bevins et al. 2012).

2.1.4 Feral cat control

There are a number of humane and efficient control methods available for feral cats (Fisher et al. 2015). When properly and efficiently done there is little distress to the animal. To determine whether a lethal control method is humane or not, the time between dispensing the method and the loss of the palebral reflex (blinking) is measured (Warburton & Poutu 2002).

There are three primary aspects to consider before embarking on a cat control operation: home range size, expected density, rate of recolonisation/population increase, and behaviour towards control methods (Parkes et al. 2014). Among the most common methods for feral cat control are shooting, poison baiting and trapping (Fisher et al. 2015). Shooting of feral and free-roaming cats is a humane method when applied skilfully and with the appropriate firearm (Parkes et al. 2014; Fisher et al. 2015). Shooting is best applied at night when a spotlight can be used to illuminate targets and diminish a cat's reactions (Fisher et al. 2015). Although shooting may be the most humane option for feral cat control, this method, overall, is time consuming and expensive and is often relegated to spot treatments of remnant populations or trap-shy individuals (Fisher et al. 2015).

Leg-hold and cage trapping are also widely used methods of cat control (Meek et al. 1995; McGregor et al. 2016). An environmental assessment in 2008 stated padded leg-hold traps followed by a humane dispatch method to be the most effective control technique (Hanson et al. 2015). This pilot study showed that although both cage traps and leg-holds were effective, leg-hold traps were up to 12-15 times more successful than traditional cage traps (Hanson et al. 2015).

Poison baiting has been a long standing method of pest control for a variety of species, but with only mixed results for feral cats (Moseby & Hill 2011; Griffiths et al. 2014; Parkes et al. 2014). Cat control using poisons is often difficult due to poor bait uptake (Moseby & Hill 2011). A majority of the success with poison baiting for cats has been in confined island areas or when their favourite prey occurs at low densities (Moseby & Hill 2011). Poison baiting programmes for feral cats have extremely variable success rates. For example, the Eradicat bait (Department of Environment and Conservation, Western Australia), applied at 10 baits

per km^2 on the Peron Peninsula, Western Australia, removed over 75% of cats (Algar et al. 2007). However, replication of this programme in South Australia resulted in a reduction of only 25% (Moseby & Hill 2011).

Bait uptake by feral cats is highest when prey abundance is low, suggesting that poison bait programmes have potential if they coincide with periods of low prey abundance, and variations in seasonal conditions (Moseby & Hill 2011). Most poison baiting for cats in NZ has been through secondary poisoning, when cats consume prey poisoned by brodifacoum. However, this is not always effective; for example, Griffiths et al., (2014) found no traces of brodifacoum in the gut contents of cats following rodent baiting on Rangitoto and Motutapu Islands, NZ. As brodifacoum accumulates in internal organs, cats may not be exposed to the toxin if primarily foraging on the muscle tissue of prey species (Griffiths et al. 2014).

Because cats are not always susceptible to secondary poisoning, new toxins have recently been trialled for primary use with feral cats. Para-aminopropiophenone (PAPP) is a relatively new toxin developed expressly for specialist carnivores, such as cats and stoats, but possibly other invasive carnivore species as well (Murphy et al. 2011; Eason et al. 2014; Glen et al. 2017). As well as a being relatively humane, this toxin has a greater effect on carnivores than on birds, potentially avoiding high numbers of non-target casualties (Murphy et al. 2011). A commercial formulation of PAPP (PredaSTOP, Connovation Ltd, Manukau) is quickly digested once administered and, thus, holds a low risk of secondary poisoning (Murphy et al. 2011). The lethal effects from PAPP are due to the rapid creation of methaemoglobin in the blood, leading to a lack of oxygen carried to the brain and muscles, followed by lethargic behaviour, lack of consciousness, then death (Murphy et al. 2011). Symptoms of PAPP ingestion are usually apparent after approximately 35 min for cats and only 10-20 min for stoats (Eason et al. 2014). Although methaemoglobinaemia can be brought on in any species, a lethal dose is achieved much more rapidly in carnivores (Eason et al. 2014). PAPP was approved in NZ in 2011 for ground control of stoats and cats using bait stations (Eason et al. 2014) . If necessary, the antidote methylene blue (methylthioninium chloride) may be used to swiftly reverse the effects of PAPP (Murphy et al. 2011). The success of poison baiting is dependent on a variety of factors, including season, weather, abundance, prey density, bait palatability, frequency of delivery and of course concentration of the toxin used (Moseby & Hill 2011). Understanding these factors and how they relate to the species will greatly enhance any poison bait control programme.

Eradication can be defined as total removal of an invasive species, and is a necessary component of mainland and island biodiversity preservation (Griffiths et al. 2014). These

operations, in general, are expensive; thus, the most efficient use of techniques is necessary to accomplish any eradication goal with the limited funding available (Nogales et al. 2013; Griffiths et al. 2014). Many control operations assume the success of their efforts by the number of animals killed (Glen et al. 2014). Cats are inherently difficult to monitor, as explained earlier. When monitoring is difficult, management is less effective. However, with the help of new monitoring techniques and statistical modelling methods, control operations are more targeted, and we may, therefore, interpret their results more accurately (Glen et al. 2014). With the rise of new control methods, such as aerial PAPP over large areas for stoats, and cats in the future; monitoring methods that are cost effective and successful at landscape scale are imperative to the future success of these operations.

2.2 Hedghogs and mustelids

Feral cats are the main target of this thesis; however, hedgehogs (*Erinaceus europaeus*), and mustelids (*M. erminea*), (*M. furo*), and (*M. nivalis*), are all an important threat to New Zealand's biodiversity, and are also of smaller focus within this thesis.

Hedgehogs are a small, primarily nocturnal, omnivorous mammal with few, if any predators, in New Zealand (Jones & Sanders 2005). Hedgehogs can weigh on average between 540-700 g, and have dispersed through most habitats in New Zealand (Jones & Sanders 2005). Home ranges can be variable, with nest sites spread throughout their home range (Jones & Sanders 2005). The average home range for hedgehogs in a pastoral location is approximately 2.5-9 ha (Campbell 1973), but may be up to 90 ha in mixed grassland locations (Jones & Sanders 2005).

Mustelids, including stoats, ferrets, and weasels, cause a significant decline among native species in New Zealand (Murphy 1996; King & Powell 2006). These animals have few predators, although weasels and stoats are vulnerable to predation by falcons (*Falco novaeseelandiae*) (King & Murphy 2005). Weasels are the smallest of the mustelids in New Zealand, preying mostly on mice (*Mus* musculus), but also birds and invertebrates (King 2005). Their home ranges can be anywhere from 1-25 ha, and densities in New Zealand are largely unknown due to dramatic fluctuations in local populations (King 2005). Stoat home ranges can be variable, and expansive, anywhere between 9 to 300 ha depending on habitat (King & Murphy 2005). Absolute density estimates for stoats are rare, but may range from 2-10 km^2 (King & Murphy 2005). Ferrets are known carriers of TB (*Mycobacterium bovis*), as well as predators of adult kiwi (*Apteryx mantelli*) (Clapperton 2005).

2.3 A brief history of current monitoring methods

2.3.1 Live capture techniques

Live capture techniques have, historically, been a successful way of monitoring animal populations and answering a host of questions about individuals within a population (Edwards et al. 2000; Russell et al. 2012; Allen et al. 2015). Live capture allows inferences to be made about many aspects of animal populations, such as abundance, density or distribution (Otis et al. 1978; Lofroth & Krebs 2007). However, this active method for studying wildlife is labour intensive, costly, and often not feasible due to geographical or logistical constraints (Castro-Arellano et al. 2008; Meek et al. 2014b; Fisher et al. 2015).

2.3.2 Tracking methods

Tracking methods have been widely used in a variety of forms for non-invasively monitoring a range of species (Zielinski et al. 2006; Olifiers et al. 2011). Although the idea of track detection is one of the oldest methods used, there have been many changes and improvements to the overall method in the late 20th century (Olifiers et al. 2011). Before the introduction of camera traps, tracking traps were one of the few non-invasive monitoring methods available to researchers (Watts et al. 2011). Original methods recorded footprints left on metal plates covered with talcum powder, a smoked-paper technique, sand plots, and white tiles with printing ink on them(Boonstra et al. 1992; Olifiers et al. 2011). Tracking techniques later favoured a tunnel design, which proved more robust against inclement weather and other elements (Olifiers et al. 2011). Tracking tunnels have been consistently used to monitor small mammals in New Zealand (Blackwell et al. 2002; Domigan & Hughey 2008) and abroad (Arthur 1999). They are able to detect footprints of a variety of different species, from large invertebrates, such as weta (*Hemideina* spp.), to medium-sized mammals, such as felids (Watts et al. 2011). Preparation generally includes inserting a pre-inked tracking card into the tunnel, with a lure placed in the centre and then left out for a predetermined period (Russell et al. 2009; Christie et al. 2015). Cat tracking tunnels are considerably larger in size than the average design meant for smaller mammals (1000 × 200 × 200 mm) vs (600 × 100 × 100 mm) (Pickerell et al. 2014). Tracking tunnels have been used successfully with feral cats as a monitoring device; however, they may struggle when occurring at low densities (Pickerell et al. 2014).

2.3.3 Scat detection dogs

Trained dogs are widely used to detect carnivores and/or their scat, (Long et al. 2007b; Glen et al. 2016). Scat detection dogs are able to cover large areas, making them a useful monitoring tool for short term, large scale operations (Gsell et al. 2010; Reed et al. 2011; Alexander 2016; McGregor et al. 2016). Scats are useful as they can provide DNA identification of individuals and a host of other information, such as diet and behaviour (Long et al. 2007a; Brown 2011). For this method, dogs are trained to associate the scent of a target species with a reward (e.g. tennis ball, food) (Long et al. 2007a). Generally, a detection team consists of a detection dog, a handler, and a navigator (Long et al. 2007a) who are responsible for one transect of a study site per survey. Long et al. (2007b) found scat detection dogs to be significantly more effective than two other methods (camera traps and hair snags) for monitoring black bears (*Ursus americanus*), bobcats (*Lynx rufus*) and fishers (*Martes pennanti*). However, two points that could be made following these results are: 1) camera trapping technology has improved and changed in the last decade; and 2) dogs have the ability to detect scats >1 day old, whereas other stationary, non-invasive methods can only detect a target species in the present time period (Long et al. 2007b). Also, the maintenance cost for a trained detection dog often supersedes the one-off purchase of a camera trap. To further investigate the effectiveness of camera traps (41 in total) compared with scat detection dogs, Glen et al. (2016) recently compared both for detecting feral cats, on two pastoral locations in New Zealand. Their results showed both methods to be comparable in cost and effort, with only small advantages and disadvantages for both techniques (Glen et al. 2016) (also see Appendix??).

2.3.4 Camera traps

Camera traps are monitoring devices that allow for non-invasive 'captures' of fauna through digital images (Swann et al. 2004; Paull et al. 2012; Meek et al. 2015). Camera trapping for research has evolved steadily over the last 20 years to become a reliable monitoring tool for a range of species (Carbone et al. 2001; Silveira et al. 2003; Rowcliffe & Carbone 2008; De Bondi et al. 2010). This method has filled a previous gap in monitoring species without the necessity of invasive procedures (Silveira et al. 2003; Glen et al. 2013; Glen et al. 2016). Camera traps are now widely used to provide information on a wealth of subjects, such as animal behaviour, occupancy, activity, and abundance (Carvalho et al. 2013; Glen et al. 2014).

Remote trail cameras come with a variety of settings and options for deployment (Meek et al. 2012; Meek et al. 2015). Cameras can have either a passive (PIR) system or an active system that sends a single beam to a separate receiver (Swann et al. 2004). Passive systems detect the rapid change in heat associated with moving animals (Swann et al. 2004; Hofmeester et al. 2016). Most cameras today use a PIR system (Swann et al. 2004). Regardless of specifications, most camera traps today feature a rugged design that allows protection from the weather elements (Swann et al. 2004).

Glen et al. (2013) compared four different camera types for detecting mustelids, hedgehogs and feral cats. This study compared detection zones, PIR vs microwave sensors, white flash compared to infrared, trigger speed and still images compared to video. Their results suggested that an infrared flash is less conspicuous to cats than a white flash, although the colour images from the white flash are clearer. Trigger speeds from 0.2–2.1 s had little effect on the capture rate of cats, but the size of the camera's detection zone did influence the success rate. Finally, they found that success rates were comparable using either video footage or still images. However, video footage required more computer memory and processing time, and more labour involved with analysing data (Glen et al. 2013). Further studies should be done to help standardise the field of view among camera traps to allow for repeatable survey methods (Glen et al. 2013; Meek et al. 2014a; Burton et al. 2015). The advantages of camera traps are prevalent/many?? especially for shy, cryptic species as they can be left for long periods of time (Swann et al. 2004; Paull et al. 2012; Glen et al. 2013). Accordingly, the use of camera traps has surpassed some traditional methods to become one of the least labour intensive options available (Carbone et al. 2001; De Bondi et al. 2010; Taylor et al. 2013).

2.4 Optimal camera trap deployment strategies

2.4.1 Orientation

Camera traps are positioned to maximise their capture success (Jackson et al. 2006; Kelly & Holub 2008; Can et al. 2011). Camera orientation, along with height from the ground, detection zone, distance from a lure (if one is used) and the size of the target species, are all considered when deploying camera traps (Glen et al. 2013; Meek et al. 2014b). Most trail cameras are placed horizontally, meaning they are parallel with the ground; with the height adjusted for the size of the target species (Smith & Coulson 2012; Taylor et al. 2013). De Bondi et al. (2010) showed an alternative placement to the typical horizontal orientation, by placing cameras vertically from the ground (at a 90-degree angle facing downwards) to capture photos from above. This technique is now known as vertical orientation (Smith &

Coulson 2012). There are advantages and disadvantages with both orientations (to be discussed in Chapter 3). While the wider field of view associated with horizontally-placed cameras may allow for greater capture rates of a target species (Taylor et al. 2013), vertical cameras set at a consistent height have a standardised field of view, allowing capture rates to be directly compared between camera locations. The smaller field of view may also help to minimise false triggers (defined as a camera triggered by anything other than a passing animal; (Glen et al. 2013)). Smith and Coulson (2012) compared vertical and horizontal orientations for two medium-sized Australian marsupials, potoroos, *Potorous tridactylus*, and bandicoots, *Isoodon obesulus*. They found that vertically-oriented cameras had up to five times more detections of these target species than the horizontal cameras. Taylor et al., (2013) performed a similar study with bandicoots, potoroos and pademelons (*Thylogale stigmatica*). Contrary to the results of Smith and Coulson (2012), this study found horizontally-oriented cameras had detections rates of up to 2.5 times greater than vertically-oriented cameras. These studies varied in both deployment and set-up methods. In addition, pademelons (4–7 kg; (Macqueen et al. 2009)) are larger than potoroos (660–1640 g (Norton et al. 2011)) or bandicoots (> 1 kg (De Milliano et al. 2016), which may influence the effectiveness of horizontal vs vertical orientation.

2.4.2 Optimal trap spacing and deployment in a landscape

Deployment strategies across a landscape, and the distance between traps, are important to the resulting detectability of a target species (Meek et al. 2014a). Feral cats often hunt in open habitats, but move throughout their home range using forest edges and scrub for cover (McGregor et al. 2015). Placing camera traps in specific areas of optimal habitat use may increase rates of detection (Mann et al. 2015; Stokeld et al. 2016). This is known as a deliberately biased placement of camera traps, and may violate some statistical assumptions by biasing detections (Meek et al. 2014a). Other deployment options include systematic placement of camera traps, e.g. placing cameras in a web or grid formation, and totally random camera placement (Meek et al. 2014a).

The distance between cameras influences the independence of observations, thus determining how the resulting data can be processed (Meek et al. 2014a). For example, spatial independence is required for most capture-mark-recapture (CMR) models and occupancy modelling studies, but non-independence is required for spatially-explicit abundance estimators (Ball et al. 2005; Chandler & Royle 2013; Meek et al. 2014a).

2.5 Statistical modelling methods: then and now

Obtaining direct counts of a population is often impossible with cryptic species that occur at low densities (Karanth & Nichols 1998; Jackson et al. 2006). Sampling of large areas also makes direct counts difficult and requires sampling sub-sets of the population (Karanth & Nichols 1998; MacKenzie et al. 2002; Karanth et al. 2011). The issue of imperfect detection is one of the most notable challenges to monitoring free-ranging populations (MacKenzie et al. 2005; Karanth et al. 2011). A multitude of different models and methods have been designed to deal with the issue of imperfect detection, from capture-mark-recapture models (Otis et al. 1978) and distance sampling (Buckland et al. 2005) (Buckland et al. 2005), to more strictly model-based methods (Royle & Nichols 2003; Royle & Young 2008). Often, traditional 'presence/absence' surveys do not correct for non-detection vs true absence (Karanth et al. 2011). However, recent studies have seen the extension of traditional occupancy models to be able to accommodate imperfect detection, habitat-specific covariates (MacKenzie et al. 2002; Mackenzie & Royle 2005; Karanth et al. 2011) and estimate detection probability (p) which, later, allows abundance estimates to be made (Royle & Nichols 2003).

The concept of population closure is an assumption often made about study systems (Pollock et al. 1990; Chandler et al. 2011). An open system acknowledges on-going immigration/emigration, births, deaths, and permanent deletions during a study and that this will influence detection probabilities, while a closed system assumes that these events do not occur during the study and that detection probabilities remain constant (Chao 1987; Pollock et al. 1990). While closed populations are simpler to understand, they are often limited to short time periods where births and deaths are not a serious consideration; thus, making them impractical for many long term population studies (Pollock et al. 1990). For highly mobile species (such as many invasive species), temporary emigration (where an individual leaves the study area within the time frame of the study, but still has the potential to return) can occur (Chandler et al. 2011). While, in reality, it is nearly impossible for closed systems to exist (Chandler et al. 2011), they allow for a highly simplified study framework with which to gain direct information about species abundance (and other information about a population) (Royle & Dorazio 2009).

2.5.1 Capture-mark-recapture

Capture-mark -recapture (CMR) is a popular method to provide relative abundance estimates for a variety of different species, especially those that are difficult to obtain counts of through other methods, such as distance sampling and line transects (Karanth 1995). Early CMR

methods involved live capture, after which animals were uniquely marked and released back into the population, with some unknown probability of recapture (Otis et al. 1978; Pollock et al. 1990; White & Burnham 1999). Although traditional CMR models were relatively limited in their ability to incorporate covariates, such as habitat heterogeneity among individuals due to behaviour, extensions of previous models now allow for these factors, plus other behavioural reactions, such as trap shyness (Hines et al. 2010). CMR requires the identification of marked individuals. Identification using camera trap images for CMR is a multi-step process that produces a 'capture' or detection history (Karanth & Nichols 1998; Jackson et al. 2006; Sarmento et al. 2009). The initial capture can be made when the image of an individual cannot be matched with another individual. Recapture occurs when the image of an individual can be confidently matched with a previously captured individual, and a null capture occurs when an image cannot be identified as either an initial capture or recapture (Sarmento et al. 2009). Most identification can be made from primary markings on the body. Some species do not have clear differences in body markings/coat patterns and secondary features (any useful marks other than primary features) may be used for identification (Jackson et al. 2006; Sarmento et al. 2009). Although use of camera traps as a CMR technique is a successful, non-invasive method, problems may arise when accounting for unmarked or partially marked individuals of a population (Chandler & Royle 2013).

2.5.2 Spatial extensions of CMR models

Recently developed extensions of the traditional CMR model are now able to account for spatial heterogeneity. A spatially-explicit capture-recapture (SECR) model allows for heterogeneity in detection probability arising from an animal's position within their home-range (Efford 2004; Chandler & Royle 2013). The detection probability changes as an animal moves about their home range, with the highest probability of capture at the centre of their home range (Chandler & Royle 2013). A scale parameter, σ, is taken from traditional distance sampling methods, and used to describe the decrease in detection probability with increasing distance from the home range centre (Ball et al. 2005; Chandler & Royle 2013). Thus, models that do not take heterogeneity into account, such as spatial distribution within a home range, may lead to a bias in the estimation of N (Chandler & Royle 2013). Typically, abundance estimates gained from detection/non-detection data come from independently spaced sample units. However, many species, especially carnivores, have extensive home ranges for which this is not possible (Ramsey et al. 2015). Unlike traditional mark-recapture models, SECR models allow non-independence between trap sites, and assume that multiple sites may be encountered within an individual's home range (Chandler & Royle 2013; Ramsey et al.

2015). Chandler and Royle (2013) developed a further extension of this model to obtain population density estimates from spatially replicated counts in an unmarked population.

The SPA model is a further extension of the Chandler and Royle (2013) SECR model, for which only detection/non-detection data from unmarked animals is available (Ramsey et al. 2015). Carnivore species are especially difficult to obtain counts from; thus, detection/non-detection data are often collected by non-invasive monitoring stations, such as scat surveys, camera traps, bait stations, hair snags and tracking traps (Ramsey et al. 2015). The ability to infer abundance estimates from detection/non-detection data may be preferable for some management programmes; hence, the demand for such statistical models (Ramsey et al. 2005; Ramsey et al. 2015).

2.5.3 Generalised linear mixed models

The use of generalised linear mixed models (GLMM) or generalised linear models (GLMS) are becoming increasingly utilized/used?? in a biological and ecological context (Quinn & Keough 2002; Nakagawa & Schielzeth 2013). Information such as the akaike information criterion (AIC) is often used as a model comparison tool for presenting these linear models and mixed-effect models (Nakagawa & Schielzeth 2013). GLMMs are an extension of linear mixed models (LMM), and form a group of models capable of including multi-level hierarchical data structures (Nakagawa & Schielzeth 2013). Often, ecological data is non-normal and involves proportions, binary (detection/non-detection), and counts that are difficult to analyse through traditional statistical modelling methods (Quinn & Keough 2002; Bolker et al. 2009).

GLMMs present a dynamic approach for analysing these types of data when random effects are present (Bolker et al. 2009). It is often more important in ecological studies to quantify the variation among sampling units due to random effects (Bolker et al. 2009). Random effects cover a range of potential contributors to variation, including individual behaviour, habitat, as well as temporal and spatial effects and sampling periods (Bolker et al. 2009). Assuming homogeneity in the variance is often unrealistic in ecological studies; however, it has traditionally been necessary to fit into the given statistical framework (Bolker et al. 2009). GLMM's allow inferences to be made with non-normal data (Bolker et al. 2009).

2.5.4 Abundance induced heterogeneity model

The abundance induced heterogeneity model (RN) of Royle & Nichols (2003) is a statistical model capable of measuring the heterogeneity of detection probability among sites and shows how this potential variation affects the probability of detecting a species at a given site.

Heterogeneity in detection probability may arise from a variety of factors, including environment, habitat-use, and behaviour. Perhaps the greatest source of variation among sites is abundance (*N*). Variation in abundance creates heterogeneity among individual sites. Variation in detection probability, *P,* is estimated by repeat surveys at the site-level. Understanding the influence *N* has on *P* allows us to extract abundance information at a site.

Tobler et al. (2015) applied the RN model to a multi-species camera trap survey. They compared the abundance-induced heterogeneity model with a more traditional occupancy model to assess changes in species richness over time (Tobler et al. 2015). The RN model was extended to account for spatial heterogeneity in detection probability (e.g. the position of a camera trap in an individual's home range, landscape, and accessibility) and also variation in localised abundance. They found the RN model to be well-suited to assessing occupancy and species richness across multiple camera trap sites over time, even when the camera trap placement changed.

Bengsen (2014) used the RN model to estimate red fox (*Vulpes vulpes*) abundance after a control effort. Abundance estimates at each station were averaged over each of the two sites for three separate 12-day periods. The RN model estimated relative fox abundance with precision post-control.

Ramsey et al. (2015) recommended the RN model and its application for estimating local relative abundance through independent sampling units (more like a traditional occupancy model) when spatial correlation due to insufficient connectivity of sampling units is not feasible. In Chapter 6 I demonstrate the use of the RN model (Royle & Nichols 2003; Bengsen 2014) for modelling the rate of detection for cats at the site level, using station-level specific variations in abundance.

Chapter 3

A comparison of horizontal versus vertical camera placement to detect feral cats and mustelids

3.1 Abstract

Invasive predators are a threat to biodiversity in New Zealand. However, they are often difficult to monitor because of the animals' cryptic, mobile behaviour and low densities. Camera traps are increasingly being used to monitor wildlife but, until recently, they have been used mainly for large species. We aimed to determine the optimal camera alignment (horizontal or vertical) for detecting feral cats (*Felis catus*) and mustelids (*Mustela furo, M. erminea* and *M. nivalis*). We deployed 20 pairs of cameras, each pair with one horizontal and one vertical camera. We compared the numbers of independent encounters with target species, numbers of photos of non-target species, and false triggers (i.e. camera triggered with no animal present) between camera orientations. Horizontally-oriented cameras captured approximately 1.5 times as many images of the target species compared with vertically-oriented cameras, and also detected more non-target animals. Orientation did not have a significant effect on numbers of false triggers.

3.2 Introduction

Invasive mammalian predators are among the greatest threats to New Zealand's biodiversity (Krull et al. 2015), but can be difficult to monitor due to their highly cryptic nature and, in some cases (e.g. feral cats), low densities (Gillies 2005; King & Murphy 2005). In recent decades, various methods have been used to assess mammals' abundance and distribution, including trapping, hair snags, spotlight counts, scat surveys, camera traps and tracking tunnels (Gompper et al. 2006; Long et al. 2007b; Pickerell et al. 2014; Lazenby et al. 2015b). In New Zealand, tracking tunnels have been the most commonly used non-lethal method for monitoring small mammals, such as rodents and mustelids (Brown et al. 1996). Although there are, indeed, many successful monitoring methods available for small to medium-sized mammals, over the last 20 years attention has turned towards camera traps as an effective research tool (Rowcliffe & Carbone 2008). Since camera traps are remotely triggered and are

impervious to most weather conditions, they may be left for long periods of time for monitoring purposes (Meek et al. 2014a; Colyn et al. 2017). Camera traps may also have higher detection rates than some other monitoring techniques, such as tracking tunnels and live capture traps (Sam 2011), and have the potential to identify uniquely marked individuals (Heilbrun et al. 2003; Sam 2011).

Numerous studies have used camera traps for large mammals, such as snow leopards (*Uncia uncia*), jaguars (*Panthera onca*) and tigers (*Panthera tigris*) (Jackson et al. 2006; Karanth et al. 2004; Kelly et al. 2008; Tobler et al. 2008; Wang & Macdonald 2009), but only a handful have examined the optimal specifications for small to medium-sized species (e.g. Bischof et al. 2014; De Bondi et al. 2010; Glen et al. 2013). There is a wide range of variables associated with camera traps, from trigger settings to sensor types as well as data analysis methods (De Bondi et al. 2010; Meek et al. 2014a). In addition, camera orientation, along with height from the ground, detection zone, distance from a lure (if used), and the size of the target species must all be considered when deploying camera traps (Glen et al. 2013; Meek et al. 2014a; Smith & Coulson 2012; Taylor et al. 2013). Camera traps are usually oriented horizontally at a height that accommodates the size of the target species (Smith & Coulson 2012). De Bondi et al. (2010) tested an alternative approach by placing cameras vertically, angled at 90 degrees, facing towards the ground to capture photos from above the target – a technique now known as vertical orientation (Smith & Coulson, 2012). This method has the advantage of standardising the size of the camera's detection zone, but this orientation may also affect the success of certain camera traps in detecting animals that encounter them.

Smith and Coulson (2012) compared vertical and horizontal orientations for two Australian marsupials, potoroos (*Potorous tridactylus*, 660–1640 g, Norton et al. 2011) and bandicoots (*Isoodon obesulus*, > 1 kg, De Milliano et al. 2016). They found that vertically-oriented cameras had detected a target species up to five times greater than horizontal cameras. Taylor et al. (2013) performed a similar study with bandicoots, potoroos and pademelons (*Thylogale stigmatica*, 4–7 kg, Macqueen et al. 2009). However, this study found horizontally-oriented cameras detected the target species up to 2.5 times greater than vertically-oriented cameras. These studies varied in both deployment and set-up methods.

We aimed to compare the effectiveness of horizontal and vertical camera trap orientations for detecting feral cats (*Felis catus*) and mustelids (feral ferrets *Mustela furo*, stoats *M. erminea* and weasels *M. nivalis*). Previous studies, such as those of Bengsen et al. (2011), and Robley et al. (2010), successfully used horizontally-oriented camera traps to detect feral cats. Horizontally placed cameras have also been used successfully with mustelids (Glen et al. 2014). As with the marsupials mentioned above, these species range in size, with

typical cats weighing 1–5 kg, ferrets 600–1200 g, stoats 200–325 g, weasels 55–125 g (Clapperton 2005; Gillies 2005; King 2005; King & Murphy 2005). We compared the number of independent encounters with the target species (stoats and cats) (Brook et al. 2012) (as distinct from repeated images of the same animal), along with the number of false triggers (when cameras were triggered without capturing an image of an animal), the total number of photos taken throughout the study (including target species, non-target species and false triggers).

3.3 Methods

The study was conducted on Toronui Station, a pastoral property in Hawke's Bay, North Island, New Zealand (39º 10′ S, 176º 46′ E). Toronui Station (1600 ha) is mainly covered by introduced pasture grass, with fragments of native beech forest (*Fuscospora solandri*), on both high country and lowland paddocks (300–1000 m above sea level). Fence lines were often hedged with pines (*Pinus radiata)* as windbreaks for livestock, which included red deer (*Cervus elaphus*), sheep (*Ovis aries*) and cattle (*Bos taurus*).

From 20 January to 24 March 2014, 20 pairs of cameras were placed along existing monitored transects. Paired camera trap sites were spaced 2.4 km apart, on average, with a minimum separation of 700 m. We placed cameras at the ecotones of forest fragments, wherever possible, to increase predator detection rates (Meek et al. 2014a). Two cameras were placed 1.5 m apart at each station. One camera was placed on a steel fence post facing vertically towards the ground from a height of 1.5 m. The other was set horizontally 7 cm from the ground (as measured to the base of the camera) and attached to a tree or wooden stake (Fig. 1). As part of a concurrent trial, rabbit meat and ferret odour (towel bedding from a male ferret's enclosure) (Garvey et al. 2017) lures were separately contained in two perforated vials, and set directly beneath the vertical-facing camera. This design allowed the lure vials to be within the field of view of both cameras.

Figure 1 Example setup of the horizontal and vertical cameras, Toronui Station, New Zealand, in 2014. Reconyx cameras and white lure vial are shown below; camera models and settings are given in Table 1

We primarily used Reconyx Hyperfire PC900 trail cameras (Reconyx Inc., Holmen, Wisconsin, USA), but also LTL Acorn 5210A (Shenzen LTL Acorn Electronics Co., Ltd, Shenzen, Guangdong, China), M990i (Moultrie, Calera, Alabama, USA) and Bushnell (Bushnell Outdoor Products, Overland Park, Kansas, USA) (see Table 1 for camera types, specifications and settings). All cameras were chosen for their infrared flash, which is likely to be less conspicuous to cats than a white flash (Glen et al. 2013; but see also Meek et al. 2014b). Vegetation was cleared to a height of 5 cm, where necessary, to provide a clear view of animals in the detection zone, and to avoid possible false triggers caused by moving branches or foliage (Kelly & Holub 2008; Taylor et al. 2013). Cameras were checked after four weeks and the batteries, memory cards (4–8 GB) and scent lures were replaced. Photos were uploaded onto an external hard drive according to their site number and orientation. All photographed animals were recorded in an Excel™ file along with any false triggers, following the methods of Allen (2014).

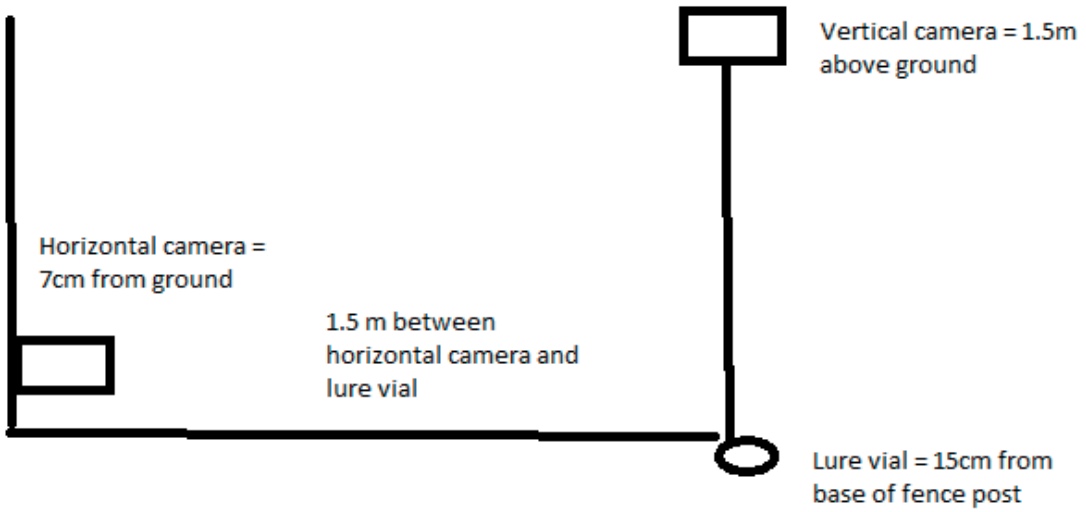


Figure 2 Dimensions of paired camera trap deployment, Hawkes Bay, North Island, New Zealand, 2015

Trigger speed can be defined as the time between a camera detecting a target and producing an image. Recovery is the time necessary for a camera to reset and prepare for the next detection event. Flash range can be defined as the area of space that the camera's light emission is able to reach. A camera's sensor detects a target in its field of view. The light source can either be infrared or white flash.

Table 1 Camera specifications and settings used at Toronui Station, New Zealand, in 2014

	Camera type			
	Reconyx ®	**LTL Acorn ®**	**Moultrie ®**	**Bushnell ®**
Trigger speed (seconds)	0.2	0.8	0.69	0.2
Recovery time (seconds)	0.5	1	5	1
Flash range (metres)	15	15	15	24
Sensor	PIR	PIR	PIR	PIR
Light source	Infrared flash	Infrared flash	Infrared flash	Infrared flash
Sense level (normal, high, low)	Normal	Normal	Normal	Normal
Number of photos	3	3	3	3

per trigger				
Number of cameras	24	10	4	2

3.4 Analysis

Photographs were classed as either: 1) target species; 2) non-target species; or 3) false trigger events. To increase the sample size, we pooled cats and mustelids for analysis simply as 'target species'. However, we will also report the results of mustelids and cats separately. We plotted histograms of the elapsed time between successive photographs of the target species to isolate encounters with an individual animal from repeated observations of the same individual (Brook et al. 2012). The mean time between consecutive photographs of cats was <10 minutes, indicating these to be repeat detections. Therefore, we assumed photographs taken >30 minutes apart were 'independent encounters' representing separate individuals, except for individuals that could be reliably identified (e.g. by coat pattern). Similarly, on the basis of the activity patterns of mustelids, (consecutive photographs <5 minutes apart) we assumed encounters >15minutes apart were independent.

We used the software program GENSTAT version 15 (VSN International 2011) to create generalised linear mixed-effects models. A Poisson error distribution was used as we had continuous count data. To assess the performance of the two camera orientations at capturing target species, camera orientation (vertical or horizontal) was fitted as a fixed effect and camera type and the camera monitoring stations were random effects. We used likelihood ratio tests to compare models with each of four response variables (numbers of target species photos, independent encounters with target species, all photos, and false triggers) to the corresponding null model without an orientation parameter.

3.5 Results

Data from 36 of the original 40 cameras were used. One camera was damaged by livestock, one was damaged by flooding and two cameras had memory cards filled to capacity, due to false triggers and livestock. The cameras detected 79 independent encounters with cats (50 on the horizontal cameras and 29 on vertical cameras), 45 independent encounters with stoats (25 horizontal and 20 vertical), and two independent encounters with ferrets (horizontal only). There were also 23 independent encounters with target species that were detected by both camera orientations. Non-target species (83% of all photos taken) included house mouse (*Mus*

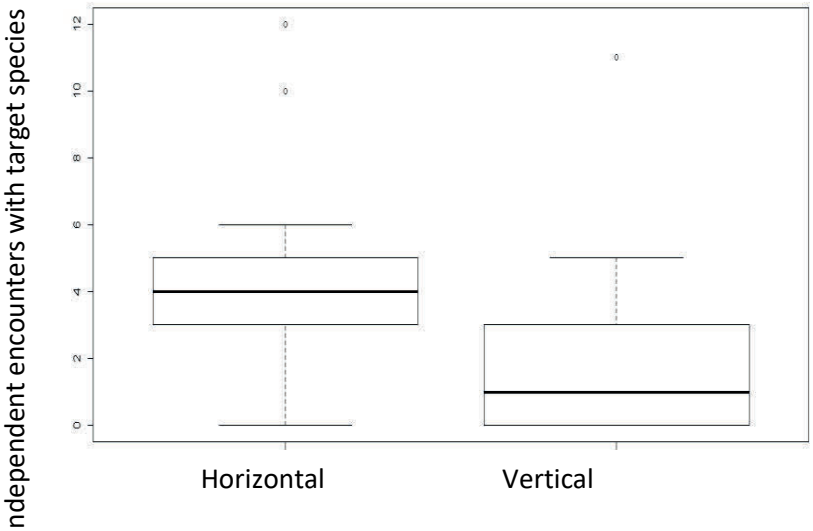
musculus), ship rat (*Rattus rattus*), Norway rat (R. *norvegicus*), brushtail possum (*Trichosurus vulpecula*), European hedgehog (*Erinaceus europaeus occidentalis*), European rabbit, feral pig (*Sus scrofa*), Eurasian blackbird (*Turdus merula*), house sparrow (*Passer domesticus*), and silvereye (*Zosterops lateralis*).

Horizontally-oriented cameras captured significantly more independent encounters with the target species than did the vertical cameras ($\chi^2 = 5.55$, df = 1, 15.4, $P = 0.032$) (Table 2, Fig. 3b), and significantly more photos in total (false triggers, target, and non-target species) ($\chi^2 = 15.67$, df = 1, 22.1, $P = 0.001$) (Table 2; Fig. 3c). However, orientation did not significantly affect the number of false triggers ($\chi^2 = 0.41$, df = 1, 16.7, $P = 0.53$) (Table 2; Fig. 3d). Vertical cameras often provided clearer images than horizontal cameras of the coat patterns of cats. However, the large body size of cats relative to the camera's field of view meant that 63% of cats photographed by vertical cameras were partially outside the frame. The corresponding proportion for horizontal cameras was 36%.

Table 2 Number of independent encounters with target species (cats and mustelids), and numbers of photos of non-target species, and false trigger events obtained from cameras with horizontal and vertical alignment, at Toronui Station, New Zealand, in 2014

Orientation	Cats	Mustelids	Non-target species	False triggers
Horizontal	50	27	22117	3746
Vertical	29	20	11478	2013

a)



b)

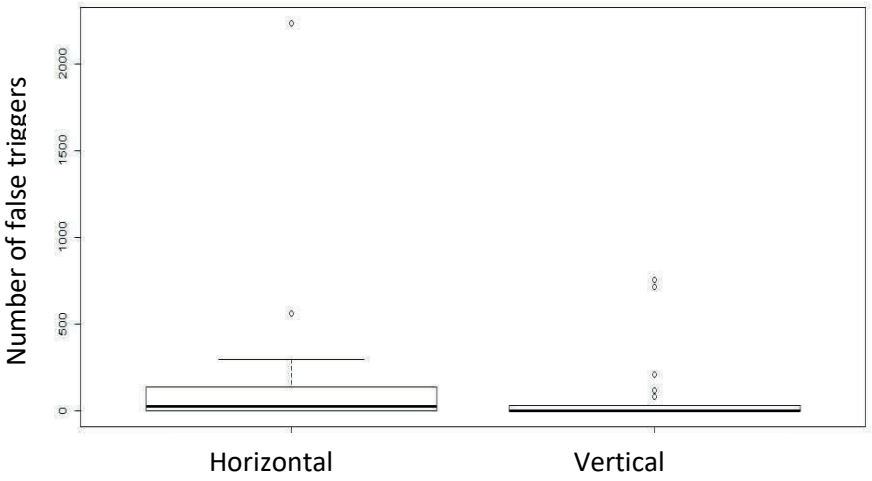


Figure 3 (a) Independent encounters with a target species (cats and mustelids); and (b) number of false triggers by cameras with horizontal and vertical alignment. Camera models and settings are given in Table 1

3.6 Discussion

Our results showed that horizontally-placed cameras were more effective at detecting the target species, i.e. cats and mustelids combined. Smith and Coulson (2012) found that the wider field of view associated with the horizontal cameras decreased detection rates for small to medium-sized species. However, their study differed from Taylor et al.'s (2013), and the present study in distance from the horizontal camera to the lure (3 m, 2 m, and 1.5 m, respectively). There was also a difference in camera settings (i.e. continuous triggering (Smith and Coulson 2012) compared to bursts of three images with a forced delay (Taylor et al. 2013).

There has been some debate over the optimal camera trap orientation for identifying individuals of a species (Smith & Coulson 2012; Taylor et al. 2013). De Bondi et al. (2010) observed that vertical cameras assisted in the species identification of mammals (smaller than cats) that fitted entirely in a camera's field of view. In contrast, although we found that cats' coat patterns were clearest in photographs taken directly beneath the vertical cameras, full coat identifications would potentially have been difficult because the cats were often only partially in the fields of view of the vertical cameras.

From these results, I concluded that horizontally-oriented cameras were more efficient at detecting feral cats and mustelids than vertically-oriented cameras. I recommend using horizontally-oriented camera traps for assessing feral cat populations. However, I suggest the possibility of raising the vertical camera and assessing its potential for use in CMR studies using dorsal coat patterns.

Chapter 4
A comparison of statistical modelling methods for evaluating a feral cat control operation using camera traps

4.1 Abstract

Accurate and precise statistical models are required to interpret camera trap data when monitoring feral cat (*Felis catus*) populations. This study assessed the ability of four different statistical models to gauge the effectiveness of a control operation targeting feral cats. Forty camera traps were placed on a pastoral property known as Waitere Station in Hawke's Bay, North Island, New Zealand. The site was subject to cat control using trapping. Cameras were on a grid with 500 m spacings, and were deployed for a total of nine weeks: pre-control monitoring, control period, followed by post control monitoring. We compared the index-manipulation-index (IMI) method; often used as a comparison for other statistical modelling methods, capture-mark-recapture (CMR); an abundance estimator using marked individuals, a generalised linear mixed model (GLMM), and a spatial presence-absence (SPA) model; that allowed individuals to encounter multiple sampling units within their home range and estimated abundance without the need for individual identification. The IMI method estimated an 85% decrease in cat abundance post-control. CMR models failed to provide accurate population estimates for this data set. The GLMM approach indicated a decrease (90%) in cat detections post-control. The SPA model estimated a decrease in cat abundance (91%) post-control, but with low precision in its estimates. The IMI method is known to be a robust measure but is of limited use as it relies on a known number of animals being removed (or added) to the population. The GLMM and SPA models both suffered from low detection rates but were still able to provide accurate estimates of the population reduction post control. Our results have implications for the future of statistical analysis of wide-scale camera trap data. The IMI method is appropriate when a known number of animals have been either removed or added to a population. The CMR method may be unsuitable in cases where recaptures are low due to poorly identifiable coat patterns. The GLMM and SPA models were successful but struggled with low precision. Examining different deployment methods, such as optimal distance and spatial formation, as well as placement in favourable habitat may increase detections.

4.2 Introduction

Efficient monitoring following control operations is vital to the success of invasive species management (Gompper et al. 2006; Bengsen et al. 2012). Complete counts of a population are seldom possible, especially for widespread or clustered species (Edwards et al. 2000; Ball et al. 2005). Accordingly, making inferences by sampling sub-sets (using direct or index methods) of the population becomes vital for monitoring over large areas (Pickerell et al. 2014). In addition, rare and/or cryptic species require appropriate, non-invasive monitoring methods that can be run over long time frames to increase detection rates (Kelly & Holub 2008; Glen et al. 2013). Surveys most often use index techniques, such as hair traps, tracking tunnels, scat surveys, chew cards, and camera traps (Ball et al. 2005; Castro-Arellano et al. 2008; Pickerell et al. 2014). These can all provide index measures of relative abundance, although all are susceptible to problems caused when the percentage of detected/captured individuals is an unknown portion of those actually present (Chandler & Royle 2013).

Camera trapping is becoming increasingly popular as a non-invasive method for monitoring elusive species (Rowcliffe & Carbone 2008; De Bondi et al. 2010; Robley et al. 2010). Camera trap deployment methods, such as settings and camera placement, vary widely depending on the target species and overall study design (Glen et al. 2013; Meek et al. 2014a) Different camera traps have a variety of features, such as passive infrared (PIR) vs active sensors, video footage vs still images, trigger speed, and flash type (infrared vs white flash) (Glen et al. 2013). Optimal camera orientation (horizontal vs vertical placement) may also vary depending on the species targeted and the overall aim of a study (Smith & Coulson 2012; Taylor et al. 2013; Nichols et al. 2017a).

Sometimes managers want to estimate absolute abundance of a species; however, previous monitoring techniques that estimate abundance often require identification of individual animals. Cameras are not always able to provide this level of detail, or animals are not individually marked and, most often, researchers are only able to estimate an index of relative abundance (Dueñas et al. 2015; Lazenby et al. 2015b). Some other non-invasive monitoring methods, such as DNA extracted from scats or hair samples (Bonner & Holmberg 2013), can also be used to identify individual animals; however, they are currently costly to collect and analyse (Sorensen et al. 2017). Detection dogs can also be used to detect elusive species; however, these require multiple years of specialised training (Glen et al. 2016). Recent advances in statistical modelling have identified approaches that may allow affordable, accurate and precise estimates of population size using camera traps, without the need for individual identification or spatial independence of monitoring devices.

Independence among sampling units may be defined as an individual detected at one sampling unit being unavailable for detection by another (Ramsey et al. 2015). The assumption of independence may be inherently violated in many studies due to the target species having large and varied home ranges, particularly in the case of carnivores (Stanley & Royle 2005; Ramsey et al. 2015).

Feral cats are found in most habitats throughout New Zealand (Gillies & Fitzgerald 2005) (Alterio et al. 1998; Gillies & Fitzgerald 2005; Glen & Byrom 2014). Feral cats have large and variable home ranges in pastoral landscapes (1-2km^2) (Langham & Porter 1991) that may overlap (Gillies & Fitzgerald 2005). Density estimates for feral cats in New Zealand are highly variable (Langham & Porter 1991; Harper 2002; Gillies & Fitzgerald 2005). However, Langham and Porter (1991) estimated feral cats at 3-6/km^2 on Hawke's Bay farmland. Feral cats are routinely targeted during predator control operations in New Zealand and elsewhere (Gillies & Fitzgerald 2005).

In this study, we used a pre-determined grid of densely-spaced camera traps along with four different statistical modelling methods to assess the change in feral cat population following control in Hawke's Bay, North Island, New Zealand. The aim was to identify the most accurate, repeatable, and precise modelling method for estimating the proportional change in the population pre- and post-control. This change can be estimated using either abundance estimates or activity indices.

4.2.1 Overview of available modelling approaches

We compared four statistical modelling methods: 1) the index-manipulation-index (IMI) method (Caughley 1977) that provides estimates of abundance; 2) capture-mark-recapture (CMR) modelling (White & Burnham 1999) that provides estimates of abundance but requires identification of individual cats; 3) a GLMM model (Bengsen et al. 2014) that provides an activity index; and 4) a spatial presence-absence (SPA) model (Ramsey et al. 2015) that also provides estimates of abundance and allows for home range estimation.

4.2.2 Index-manipulation-index (IMI) method

The IMI method estimates absolute abundance of a local population, by obtaining two indices of population size, a baseline estimate and a second estimate after a known number of animals have been removed (Caughley 1977; Fryxell et al. 2014). This method is traditionally used over a short period of time, as it assumes a population being assessed is closed to all births, deaths, immigration, or emigration (Fryxell et al. 2014). A study by Edwards *et al.* (2000) suggested the IMI method be used to test the accuracy of other methods for estimating

populations of feral cats and other carnivores. The IMI method is labour intensive due to the necessity of obtaining two indices (Edwards et al. 2000), (Edwards & Ealey 1975) but was made feasible in the current study by a baseline monitoring effort through camera trapping, followed by an intensive removal period, and then a second monitoring effort with camera traps.

4.2.3 Capture-mark-recapture (CMR) model

CMR modelling techniques have long been a staple method for estimating the population numbers for a variety of carnivore species (Chapman & Balme 2010). However, the intensive labour involved in physically capturing, marking and recapturing animals has led to an increase in non-invasive monitoring methods, such as camera trapping, which perform well when monitoring elusive species that may become trap shy (such as most felids) (Karanth 1995; Karanth & Nichols 1998; Chapman & Balme 2010). Some of the first studies to use CMR methods with camera traps monitored large wild felids, such as tigers (*Panthera tigris*) (Karanth 1995), jaguars (*Panthera onca*) (Soisalo and Cavalcanti 2006), and snow leopards (*Uncia uncia*) (Jackson *et al.* 2006; Karanth 1995; Karanth and Nichols 1998). While some big cats are easily identifiable by their unique coat patterns, this does not apply to populations that lack clear and unique markings (Chandler and Royle 2013). We sought to quantify whether this technique was applicable for monitoring much smaller and more uniformly marked feral cats. In addition, we could directly compare photos with all cats that were removed from the study site by contractors following control work.

4.3 GLMM method

A generalised linear mixed model (GLMM) method has been used previously to compare numbers of red fox (*Vulpes vulpes*) observations with a Poisson error distribution and log link to produce an activity index, i.e. (Bengsen et al. 2014). Observations were counted when separated from the preceding observation by > 1 h (Bengsen et al. 2014). In a situation such as a management operation, the GLMM method assumes any variation in detectability to be of less significance than the change caused by the management operation itself (Bengsen et al. 2014). We can safely assume this when survey effort (camera trapping) is consistent across the time period these efforts do not change the animal's behaviour, and there is no seasonal variation that may influence behaviour (Bengsen et al. 2014).

4.4 Spatial presence absence model (SPA)

To monitor feral cat abundance in this study we tested an extension of the spatial capture-recapture (SCR) model (Chandler & Royle 2013; Royle et al. 2013). Chandler and Royle (2013) applied the SCR model to avian point-count data to obtain a population estimate. The model successfully estimated population density; showing that neither individual recognition, nor spatial independence is needed to determine density. Similarly, the SPA model allows for a variety of non-invasive devices; such as bait stations or camera traps, to sample individual encounters that are non-independent (Ramsey et al. 2015). We applied this model (SPA) to the detection/non-detection data rather than count data. The model estimates the spatial detection parameters g_0 (probability of detecting an animal at the centre of its home range on one night), σ (the rate at which detection probability declines with increasing distance from the home-range centre), along with abundance (N) of a target species. Accordingly, home range size is taken into account while deploying sampling devices so that multiple devices will assumed to be encountered by a single individual within its home range. Previousdistributions are required in order to explain the detection parameters and these can either be informative or uninformative, depending on the target species and what information is available (Ramsey et al. 2015). Although used previously to estimate abundance of red foxes (*Vulpes vulpes*; Ramsey et al. 2015), the SPA model has yet to be trialled on detection data for feral cats.

4.5 Materials and methods

?????

4.6 Study sites

Waitere Station is a pastoral farm in Hawkes Bay, North Island, New Zealand (~39º S, 176º E) with small patches of native bush throughout. The site had no recent history of predator control and the study took place from April to June 2014. In total, 40 Reconyx PC 900 (Reconyx Inc, Holmen, Wisconsin) cameras were deployed in a 7 km^2 grid with c. 500 m spacing between individual cameras. In case of hazardous terrain or close proximity to livestock/roads there was a lenience/allowance made?? of $\pm$ 100 m at each site.

All cameras were mounted on wooden stakes with the base of each camera 5 cm from the ground. All cameras were set to take a series of three photos per trigger, with no delay between triggers. A lure of male ferret (*Mustela furo*) odour and rabbit (*Oryctolagus cuniculus*) meat (Ramsey et al. 2015; Garvey et al. 2017; Nichols et al. 2017a) was placed in a

vial 1.5 m in front of the camera and secured with a tent peg. The use of ferret odour as a portion of the lure was part of a concurrent trial, but had previously been shown to be attractive to a range of carnivores, including cats (Garvey et al. 2017). Cameras were deployed for a total of nine weeks and predator control was carried out in Weeks 4–6 of camera deployment. A camera trap 'night' was deemed the 24 h period from midnight to midnight. Predator control consisted of removing targeted mammalian pest species from a defined area. Although feral cats were the primary target species for control, other predators, such as mustelids (*M. furo, M. erminea,* and *M. nivalis*), rats (*Rattus* rattus) and hedgehogs (*Erinaceus europaeus*), were also removed during the operation. Specialist contract trappers removed cats and other species using a combination of cage, leg-hold and kill traps. Live traps were checked daily soon after sunrise, captured animals were humanely killed, and all carcasses collected. The predator control was part of a routine management programme by the Hawke's Bay Regional Council. The three week monitoring periods in the following sections are referred to as 'pre-control' and 'post-control'.

4.7 Data analysis

4.7.1 IMI method

The IMI method calculated population size using two indices, I_1 (the pre-control estimate, calculated from number of camera sites detecting cat activity) and I_2 (the post-control estimate, calculated from number of camera sites detecting cat activity) after a known number of individuals were trapped and removed, C (Fryxell *et al*. 2014). The population estimate (Y_1) can then be measured as follows:

$$Y_1 = I_1 C / (I_1 - I_2)$$

The proportion of animals removed can be defined as $p^* = (I_1 - I_2) / I_1$, with the proportion of animals remaining shown as $q^* = 1 - p^*$. From this the variance can be calculated by:

$$\mathrm{Var}(Y1) \approx Y_1^2 (q^*/p^*)^2 (1/I_1 + 1/I_2)$$

4.7.2 CMR method

For CMR, individual detection histories were created for identifiable cats and analysed using the program MARK® version 8.2 (White and Burnham 1999). Cats were identified based on coat pattern and/or other unique morphological features. A closed-capture model was used to estimate cat abundance pre-predator control; with the assumptions that no animals

immigrated/emigrated from the local population over the nine weeks of the study. We then ran MARK using models M0 (assumes no variation in capture probability), Mb (assumes a different capture probability for unmarked and previously marked individuals, but otherwise there was no variation in capture probability), and Mt (assumes variation in capture probability from one sampling occasion to the next, but permits no variation among individuals within an occasion) (Karanth & Nichols 1998). However, due to the small sample size of identifiable cats (n = 5), more complex models, such as Mh, Mtb and Mtbh, were unable to converge. Due to the low number of identifiable cats and the associated low statistical power we have not presented any abundance estimates in the Results section.

4.7.3 GLMM method

The GLMM method was used to detect changes in cat detections pre- and post-control. Cat detections were denoted by a '1' per camera trap night while non-detections were denoted by a '0'. Although the model was originally designed to examine changes in numbers of detections (with a Poisson error distribution), so instead we calculated the % rate of detection averaged across all cameras at the site, due to such low numbers of detections. Thus, we ran the model with a binary response variable. We used a binomial distribution and estimated the mean rate of detection across all cameras at the site, pre- and post-control. Fixed effects in the model was the control period with camera station number noted as a random effect. The model was fitted in R 3.1.1 (R Development Core Team 2016) using a code adapted from Bengsen *et al.* (2014).

4.7.4 SPA model

We also analysed cat detections using a Bayesian model that allowed the use of detection/non-detection data to estimate abundance (Ramsey et al. 2015). A spatially-explicit model of the detection probabilities was fitted to the detection data, enabling estimates of abundance (N) as well as the spatial detection parameters g_0 and σ (see above).

The model was fitted using JAGS 3.3.0 (Plummer 2003) called from R 3.1.1 (R Development Core Team 2016) using code adapted from (Ramsey et al. 2015). Based on a review of published information on possums (*Trichosurus vulpecula*), ferrets (*Mustela furo*), and stoats (*Mustela erminea*) home ranges and movements (Glen & Byrom 2014) an informative prior was used for the home range scale parameter (σ) using a gamma distribution with values (4.5, 0.01). These values result in a mean value for σ of 450 m (95% CI 135-950 m). Using the same study data an informative prior of was also used for per occasion probability of detection parameter (g_0) using a beta distribution with values (1,5). These

values result in mean value for g_0 of 0.16 (95% CI 0.00-0.52). Finally, we used an upper limit for population size N (used for data augmentation; Ramsey et al. 2015) of 200 for the entire control area. Cat densities vary hugely worldwide with values of 1-30/km^2 for cats living independently of humans (Liberg et al. 2000; Turner & Bateson 2000). The study area (with no buffer added to the cameras on the edges) is approximately 7 km^2 so that an upper value of 200 is an extreme biological maximum.

4.8 Results

4.8.1 Camera detection

Of the 40 cameras deployed, 39 remained operative throughout the study period. There were 106,832 photos taken across both periods on Waitere Station (226 of cats pre-control and 31 post-control). The contract trappers removed 17 cats from Waitere Station during the control period. Cameras detected cats on 19 occasions at 13 of 40 locations during the pre-control period. In the post-control period two cats were detected at two of 39 locations (Fig. 4).

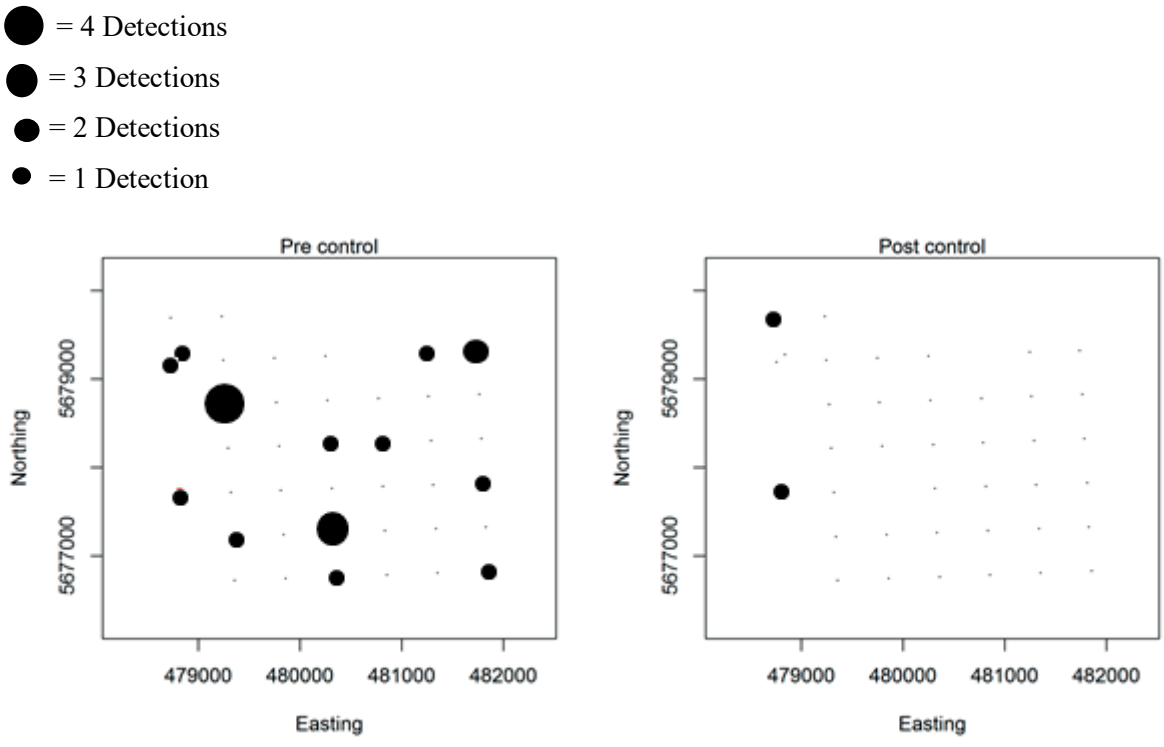


Figure 4: Cat detections at Waitere Station, North Island, New Zealand pre- and post-control. Dots indicate cameras that detected one or more cats, and size of the dot indicates the number of detections.

4.8.2 IMI method

According to the IMI method, the removal of 17 individuals led to an 89% reduction in feral cats (Caughley 1977; Fryxell *et al.* 2014). We estimated there were 20 (SE ± 18) cats on Waitere Station in the pre-control period and two to three animals survived post-control.

4.8.3 GLMM method

The GLMM indicated very strong evidence for a decrease in cat detections after predator control at ($P < 0.001$) on Waitere Station. Detections decreased from 1% for the pre-control period to 0.1% post-control providing an approximate population reduction of 90% (Fig. 4).

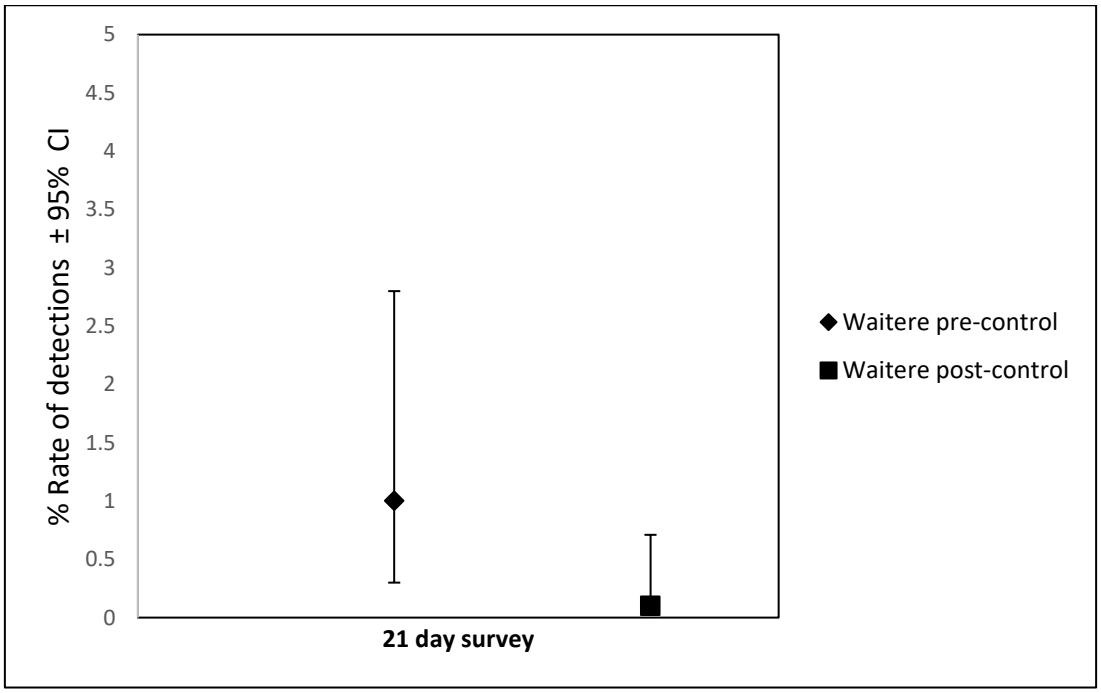


Figure 5 Rate of detection of feral cats per camera (with 95% CI) in the pre- and post-control periods at Waitere Station, North Island, New Zealand

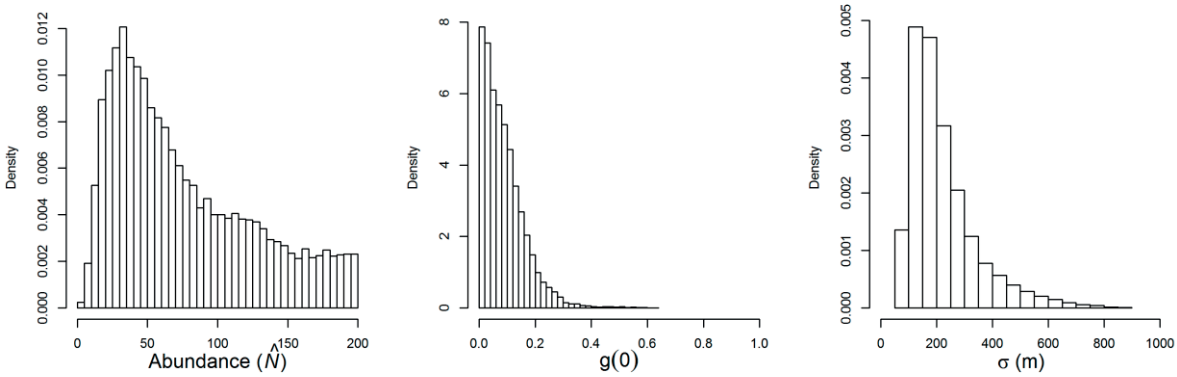
SPA Model

The SPA model (Ramsey et al. 2015) estimated a median population of 33 cats ($g_0 = 0.07$ and $\sigma = 188.2$ m) on Waitere during the pre-control period and three cats in the post-control period, which is a reduction of 91% ($g_0 = 0.01$ and $\sigma = 265.4$ m) (Table 3; Fig. 5).

Table 3: Estimates with 95% confidence intervals in brackets for Waitere Station, North Island, New Zealand.

Parameter	Pre-control	Post-control
N	33 (9 – 181)	3 (1 – 170)
g_0	0.073 (0.0017 – 0.227)	0.013 (0.00006 – 0.121)
σ	188.21 (58.67 – 478.97)	265.37 (52.01 – 623.29)

a)



b)

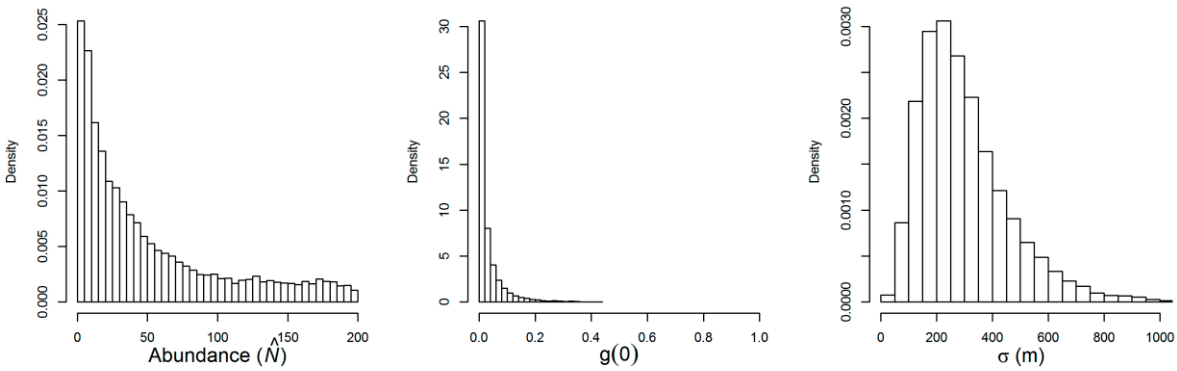


Figure 6: Estimated abundance (N) and spatial detection parameters (g0 and σ) of feral cats at Waitere Station, North Island, New Zealand in the pre-control (a) and post-control (b) periods

4.9 Discussion

Gauging the success of a control operation is important for wildlife management. Camera traps continue to be a successful, non-invasive detection device suitable for monitoring elusive species, such as feral cats (Bengsen et al. 2011; Brassine & Parker 2015; Stokeld et al. 2016). This study compared multiple statistical models to estimate changes in feral cats' activity and abundance from camera traps in a pastoral landscape, pre- and post-predator control. With feral cats having an expected home range of 1-2 km^2 (Langham & Porter 1991) in this landscape, camera traps spaced at ~500 m apart are considered non-independent. This allows the use of the SPA model, a Bayesian model that gives estimates of detection probability and abundance based on detection/non-detection data from spatially-correlated sampling units (Chandler & Royle 2013; Ramsey et al. 2015); however, the SPA model requires high numbers of detections and multiple encounters with a sampling unit to give accurate and precise estimates.

The IMI method estimated a pre-control population of 20 cats at Waitere Station. With the removal of 17 cats, we estimated a population reduction of 85%. This was most likely the most accurate population estimate provided (see below). While this method requires two measures (trap catch and an activity index) – this could be a simple method for field managers to use if they want to quickly estimate the success of a cat control operation. However, caution should be taken, as unlike the other models used here; this method is unable to account for precision in the observational process, nor for imperfect detection. The GLMM method estimated a similar reduction in cat detections of 90% following control but with very low precision. While the precision was low, this method of estimating reductions in population was accurate and the technique was useful; therefore, in estimating changes in target species activity following control, as also seen in (Bengsen et al. 2014). The SPA model estimated a pre-control population of 33 cats, with an estimated population reduction of 91%, leaving three cats post-control. With a known number of cats removed from the population (n = 17), the SPA model's pre-control estimate is higher than expected; however, this is unsurprising due to the overall low numbers of multiple detections across the site.

Using an informative prior for σ (Glen & Byrom 2014) the SPA model was able to estimate the home range size the local population of feral cats. The model converged on a pre-control home range estimate of 0.72 km^2 and 1.42 km^2 post-control. Similar results have been found for possums, with home ranges shifting and increasing in size after a control operation (Efford et al. 2000). The SPA model's home range estimates were lower than previously found in other feral cat studies in NZ (Gillies & Fitzgerald 2005), but similar to those

estimated by Langham and Porter (1991) in a similar habitat on Hawke's Bay farmland. The results from the CMR model were not reliable as the sample size of identifiable cats was insufficient. Although CMR using camera traps has been previously successful with other wild field populations, the similarity in coat patterns between some feral cats made this approach unsuitable for our purposes.

The overall low precision for the GLMM method and SPA model were mostly due to the low numbers of detections pre- and post-control. Accounting for the SPA model's home range estimates, and the fact that cameras were deployed at a density of one camera per 0.25/km^2, the problem with low detections was surprising. This issue of low detections relates to g_0 – where we used an informative prior of 0.16, based on Glen and Byrom (2014), with the assumption that feral cats would likely be more trappable than other predators, such as stoats (*Mustela erminea*) and ferrets (*Mustela furo*). The SPA model converged on a g_0 of 0.07 pre-control and this decreased to 0.01 post-control suggesting that feral cats may be less trappable than previously thought. These camera trap surveys should have been longer; however, if they were much longer, the assumption of closure within the population could be violated (Glen et al. 2016). Effective monitoring methods do not necessarily resolve problems associated with low detection (MacKenzie et al. 2005) as there are a number of unobservable causes for variation among detection rates; such as behavioural preferences and overall abundance (Dorazio & Royle 2005). However, deploying clusters with multiple cameras (Stokeld et al. 2016) and/or strategically placing cameras in favourable predator habitats (Glen et al. 2017) may substantially increase detections.

In conclusion, camera trap data may be analysed in various ways to estimate cat activity and abundance. While the SPA model was able to estimate animal abundance at a localised scale of a few square kilometres, it required intensive sampling and struggled with the low numbers of individuals and multiple detections. The GLMM method was able to cope with the low detections; however, it only provided a rate of detection, and the change thereof, rather than a measure of absolute abundance. Also, deploying multiple sampling units within any potential individual's home range means the camera trap stations were spatially non-independent. This, potentially, violates an assumption of the GLMM, which was the independence of sampling units. If there had been a substantially higher number of cat detections, this model may have been positively biased as individuals would be expected to encounter multiple sampling stations within their normal home range.

Using a spatially-explicit presence-absence model to estimate hedgehog (*Erinaceus europaeus*) density

Chapter 5

Abstract

Hedgehogs (*Erinaceus europaeus*) are an important threat to native biodiversity in New Zealand. Although regular control efforts include hedgehogs as a target species, there remains relatively little information on their densities in landscapes across New Zealand.

In order to gauge the success of a control operation, efficient monitoring devices must be in place to gather pre- and post-control estimates. Camera traps are an efficient, non-invasive monitoring device that can provide a wealth of information about a target species. Accurate and precise statistical modelling methods are required to interpret camera trap data when monitoring hedgehog populations.

This study assessed the ability of a spatial presence-absence (SPA) model to estimate hedgehog density pre- and post-predator control operation, using camera traps as monitoring devices. The SPA model is a Bayesian approach that does not require the identification of individuals, but does assume spatial correlation between detection devices to allow multiple encounters within an individual's home range.

A total of 40 cameras were placed on a pastoral property in Hawke's Bay, North Island, New Zealand. Waitere Station was subject to intensive predator control using a variety of leg-hold, cage, and kill traps. All cameras were on a pre-determined grid with 500 m spacing. The cameras were deployed for a total of nine weeks: 1) pre-control monitoring period of three weeks; 2) followed by three weeks of intensive predator control; and then, 3) three weeks of post-control monitoring. The intensive trapping period was part of a parallel study aimed at feral cats; however, hedgehogs were also trapped and removed.

The SPA model estimated a reduction of 60% in the hedgehog population on the treatment site after three weeks of intensive trapping (N = 105 pre- control and N = 38 post-control). Although, unlike cats in Chapter 4, where a known number of individuals had been removed allowing the IMI method to be used, we do not have the same data for hedgehogs (as they were not the target of the operation). However, trappers regularly commented on the high numbers of hedgehogs they were catching in their cage traps.

The SPA model is a capable statistical model for estimating changes in hedgehog density, and successfully showed the effect of a control operation on hedgehog abundance.

5.1 Introduction

The European hedgehog (*Erinaceus europaeus*) is a small mammal that was first introduced to New Zealand in the late 1800s (Jones & Sanders 2005). They have since dispersed throughout the temperate portions of the mainland and many offshore islands (Jones & Sanders 2005). Hedgehogs are nocturnal, solitary and have variable home-ranges (0.02 - 0.5 km^2, although some individuals have been known to utilise/roam?? up to 1 km^2. Home-range size may also differ among seasons, especially where hibernation occurs due to colder weather (Jones & Sanders 2005). Hedgehogs prefer coastal pastoral land, but may be found in higher elevations, as well as up to 14% of New Zealand's braided river systems (Jones & Sanders 2005) and throughout suburban developments.

In comparison with New Zealand's other mammalian predators, such as mustelids (*Mustela furo, M. erminea,* and *M. nivalis*), brushtail possums (*Trichosurus vulpecula*), feral cats (*Felis catus*) and ship rats (*Rattus rattus*), hedgehogs have seldom been studied; perhaps because they may be perceived as a lesser threat to biodiversity than these other predators. However, their high numbers in comparison to the previously mentioned pest species potentially make them an ever greater threat to biodiversity. While they are primarily insectivorous, hedgehogs are known to eat any animal-based substance, in particular, mice (*Mus musculus*), lizards, frogs, and many ground-dwelling birds (Jones & Sanders 2005). Hedgehogs are implicated in the decline of North Island brown kiwi (*Apteryx australis mantelli*) chick survival (Berry 1999b), black-fronted terns (*Sterna albostriata*), wrybill (*Anarhynchus frontalis*) and black stilts (*Himantopus novaezelandiae*) (Jones & Sanders 2005).

Not only do hedgehogs prey on a variety of New Zealand native wildlife, but they may also compete with ground dwelling birds, such as the North Island brown kiwi for nest sites and food (Berry 1999a; Jones & Sanders 2005). Hedgehogs prefer nesting under dense vegetation, logs, old rabbit burrows (Recio 2016), which are also the preferred nesting sites for kiwi (Berry 1999b). Both hedgehogs and kiwi form home ranges based primarily on similar food resources; thus, conflicts may occur as hedgehog populations increase over time (Berry 1999b). Hedgehog numbers are able to remain high due to their high fecundity, few natural predators, high tolerance to toxins, such as brodifacoum, (Berry 1999a), and seasonal inactivity (Griffiths et al. 2015). The literature suggests local densities of hedgehogs to be anywhere from ~0.69 – 5.5 ha^{-1} (Berry 1999b; Bowie et al. 2010).

Numerous studies have examined hedgehog movements and use of habitats (Shanahan et al. 2007; Recio et al. 2011; Griffiths et al. 2015) but there are few population density estimates for hedgehogs in New Zealand (Jones & Sanders 2005) compared with European studies (Young et al. 2006; Trewby et al. 2014). Hedgehogs are a threat to native biodiversity not only in their competition for resources but also in direct predation of ground-dwelling birds, such as black stilt (*Himantopus novaezelandiae*) (Recio 2016), and many other endangered native species, such as grand skinks (*Oligosoma grande*), Otago skinks (*O. otagense*) (Reardon et al. 2012), the robust grasshopper (*Brachaspis robustus*), and weta (*Hemiandrus* spp.) (Jones et al. 2005).

The primary method for estimating hedgehog populations has been capture-mark-recapture (CMR) (Parkes 1975; Jackson & Green 2000) and success rates from kill trapping (Glen et al. 2014).

Trapping and tracking methods for assessing relative abundance indices have been common (Jones & Sanders 2005) but they are labour intensive over long term surveys (Glen et al. 2014). Glen et al. (2014) found camera traps are more suitable than kill trapping methods for measuring the relative abundance of hedgehogs.

There are variety of camera trap models and deployment settings available. A previous camera trap study by Glen et al. (2013) gave optimal settings and a procedure for capturing images of hedgehogs and other predators, such as by using a passive infrared sensor, still image over video, infrared flash, and a trigger speed of up to 1.6 s (Glen et al. 2013; Glen et al. 2014).

The spatial presence-absence (SPA) model is a Bayesian approach that has been used to estimate feral cat and red fox (*Vulpes vulpes*) densities without the need for individual identification (Ramsey et al. 2015). This model is an extension of the spatial-capture-recapture model (SCR) (Chandler & Royle 2013), which was applied to avian point count data. The SPA model allows for a variety of different non-invasive, remotely deployed monitoring devices that provide detection/non-detection data (Ramsey et al. 2015). The model also assumes the devices are set non-independently, meaning multiple devices may be encountered by the same individual within their home-range. The model estimates σ (the rate at which detection probability declines with increasing distance from the home-range centre), spatial detection parameters g_0 (daily probability of detecting an animal at the centre of its home range) and the abundance (N) of a target species.

In Chapter 5, I deployed a high density of camera traps (40 ~ 7 km^2) over a pastoral site in Hawke's Bay to monitor feral cats pre- and post- a predator control operation. I compared the effectiveness of the SPA model with other methods (index-manipulation-index

(IMI) method, capture-mark-recapture (CMR), and a generalised linear mixed model (GLMM) to measure feral cat abundance and rates of detection pre- and post-predator control. While the SPA model was highly accurate and gave similar estimates as the IMI method, (SPA ~ 24 cats estimated pre-control and two post-control, IMI ~ 20 cats pre-control and three post-control), there was a wide variation in the SPA estimates (13-185 cats pre-control, and two to 184 cats post-control). The SPA model requires multiple detections at each station to create a spatial connectivity network. This may be more feasible with hedgehogs that occur at higher densities.

Specialist trappers used a combination of cage, leg-hold, and kill traps to remove feral cats and mustelids. Although hedgehogs were not a target species, there was no attempt to limit their access to the traps and previous work suggests both cage and kill trapping to be a highly successful method of control for hedgehog populations (Bowie et al. 2010). Bowie et al. (2010) had success using cage traps and Fenn traps (set for mustelids) for eradicating a low-density population of hedgehogs (0.69 ha^{-1}) from Quail Island reserve, Banks Peninsula, New Zealand over multiple years.

5.2 Materials and methods

Study site

Waitere Station is a pastoral farm in Hawkes Bay, North Island, New Zealand (~39º S, 176º E) with small patches of native bush throughout. The site had no recent history of predator control and the study took place from April to June 2014. In total, 40 Reconyx PC 900 (Reconyx Inc, Holmen, Wisconsin) cameras were deployed in a 7 km^2 grid with c. 500 m spacing between individual cameras. In case of hazardous terrain or close proximity to livestock/roads there was a lenience of $\pm$ 100 m at each site.

All cameras were mounted on wooden stakes with the base of each camera 5 cm from the ground. All cameras were set to take a series of three photos per trigger, with no delay between triggers. A lure of male ferret (*Mustela furo*) odour and rabbit (*Oryctolagus cuniculus*) meat (Ramsey et al. 2015; Garvey et al. 2017; Nichols et al. 2017a) was placed in a vial 1.5 m in front of the camera and secured with a tent peg. The use of ferret odour as a portion of the lure was part of a concurrent trial, but had been shown previously attractive to a range of carnivores, including cats (Garvey et al. 2017). Cameras were deployed for a total of nine weeks and predator control was carried out in Weeks 4–6 of camera deployment. A camera trap 'night' was deemed the 24 h period from midnight to midnight. Predator control consisted of removing targeted mammalian pest species from a defined area. Although feral cats were the primary target species for control, hedgehogs and other predators, such as

mustelids (*M. furo, M. erminea,* and *M. nivalis*), rats (*Rattus* rattus) were also removed during the operation. Specialist contract trappers removed cats and other species using a combination of cage, leg-hold and kill traps. Live traps were checked daily soon after sunrise, captured animals were humanely killed, and all carcasses collected. The predator control was part of a routine management program by the Hawke's Bay Regional Council. The 3-week monitoring periods in the following sections are referred to as 'pre-control' and 'post-control'.

5.3 Analysis

SPA model

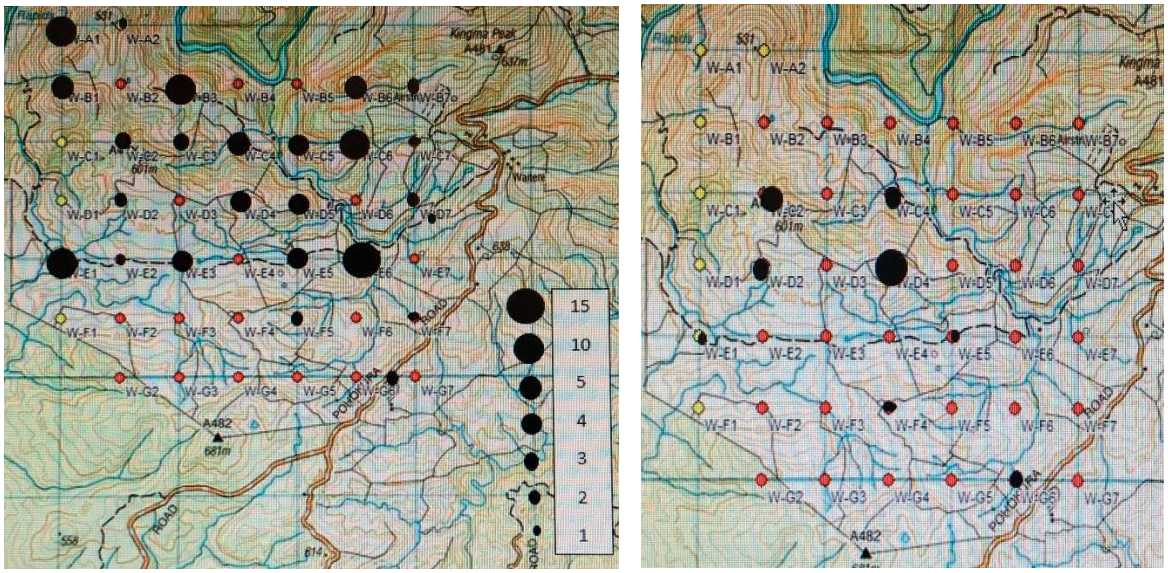
We analysed hedgehog abundance using the SPA model, a spatially explicit model that uses detection/non-detection data (Ramsey et al. 2015). A spatially-explicit model of the detection probabilities was fitted to the detection data, enabling estimates of abundance as well as the spatial detection parameters g_0 and σ (see above).

The model was fitted using JAGS 3.3.0 (Plummer 2003) called from R 3.1.1 (R Development Core Team 2014) using code adapted from (Ramsey et al. 2015). Based on a review of published information on hedgehog home ranges (Jones & Sanders 2005), an informative prior was used for σ; however, an upper limit of population size, N, (used for data augmentation; Ramsey et al. 2015) was set at 200 for each area to ensure realistic estimates were derived. An informative prior of 0.05 was used for g_0, as this has been used previously with possums (Ball et al. 2005).

5.4 Results

5.4.1 Camera detections

Of the 40 cameras deployed, 39 remained operational throughout the study period. There were 106,832 photos taken across both periods on Waitere Station (1,591 hedgehogs pre-control and 266 post-control). Hedgehogs occurred (as defined by an independent encounter, > 30 min between camera triggers) 115 times at 25 camera trap stations during the pre-control period, and 26 times at nine camera trap stations on Waitere Station. (Fig. 7a,b).



a). b).

Figure 7 Hedgehog detections during the pre-control period (a) and post control period (b) on Waitere Station, North Island, New Zealand, 2015

5.4.2 SPA model

The SPA model estimated a population of 105 hedgehogs (g0 = 0.51 and σ = 119 m) during the pre-control period and 38 hedgehogs in the post-control period (g0 = 0.55 and σ = 105 m) (Table 4).

Table 4 Estimates of mode for N and means for g0 and σ for hedgehog populations with 95% CI

Parameter	Pre-control	Post-control
N	105 (31-185)	38 (8-105)
g0	0.51 (0.31-0.77)	0.55 (0.25-0.90)
Σ	119 (74-197)	105 (51.2-188)

5.5 Discussion

Camera traps have proven an effective monitoring device for small to medium sized mammals and were an effective tool to use to obtain detection/non-detection data for hedgehogs. The SPA model has shown potential to estimate abundance for this species. In the previous chapter, the SPA model was applied to feral cat detection data from the same high density grid of camera traps. This model is sensitive to sample size and had low precision when applied to a target species that naturally occur at low densities. However, the hedgehogs in

this area occur in higher numbers than cats and the SPA model appears well suited to this data set.

As mentioned previously, there are few population estimates for hedgehogs in New Zealand (Jones & Sanders 2005). Previous estimates of marked individuals on a golf course in Lower Hutt, Wellington, New Zealand found hedgehogs at approximately 1.75/ha (Parkes 1975). However, Berry (1999) found hedgehogs at a density of 5.5/ha around Boundary Stream, Hawke's Bay, New Zealand. The home range size for hedgehogs is highly variable in the literature (Jones et al. 2005). Most estimates range from 2-50 ha, with some up to 100 ha. Berry (1999) saw seven radio-tagged hedgehogs move an average of 908 m per night in Hawke's Bay (anywhere from 477-2264 m). This is unsurprising when hedgehogs are noted to have multiple den sites (Jones & Sanders 2005). However, due to the high variability in home range size and distance traversed in any given night, there is a possibility the SPA model's requirement for non-independent sampling units may have been violated. If this were indeed the case, then analysing the data using the RN model could be applicable (Ramsey et al. 2015) (Chapter 6). However, many hedgehogs (pers. comm. by specialist trappers) were removed through cage trapping during the control operation aimed at feral cats; and the SPA model did estimate a population reduction. Detection events taken from camera trap images were consistent with density estimates obtained from the SPA model, as also seen in Chapter 5.

According to Bowie et al. (2010), cage trapping and kill trapping must be used intensively over consecutive years in order to achieve an extreme decrease in hedgehog numbers. While a 60% reduction in abundance may not be substantial compared to other control operations, we must keep in mind this species was not the primary target for trappers. Thus, we were impressed with the reduction in population over a short time and have contributed to the understanding a prolific invasive predator.

Chapter 6 An evaluation of strategically and widely spaced camera traps for monitoring feral cats

Abstract

I deployed camera traps to monitor a feral cat (*Felis catus*) population prior to a predator control operation, as part of the *Cape to City* ecological restoration project, near the East coast of the North Island, New Zealand. Surveys took place across two neighbouring sites, both destined for control. Cameras were spaced widely with 2-km spacing, in habitat associated with high encounter rates for cats. I aimed to maximise detections of feral cats by placing cameras in these habitat 'hot spots' as compared to the detection probabilities from Chapter 4 (~1%) using cameras set out on a pre-determined grid. Analysis for the current study used a generalized linear mixed model (GLMM), to compare camera trap detection rates for feral cats at both sites, as well as an abundance-induced heterogeneity model (RN) to calculate detection probabilities and relative abundance of cats at both sites. The RN model also examined the effects of habitat type on detection probability based on habitat type as not all cameras could be placed in hot-spot locations. The GLMM method estimated detection rates of 5.2% (95 % C.I 2.3-7.9) for site 1, and 4.3% (2.6-10.3) for site 2. The RN model estimated detection probabilities of 5.5% (95% CI 4.1-6.9) for site 1, and 4.5% (3.1-5.9) for site 2. The RN model also estimated an average relative abundance of 12.6 (6.9-22.8) feral cats on site 1, and 8.3 (4.6-14.9) on site 2. The RN model indicated variation in detection probabilities by habitat type, through increased relative abundance at camera traps placed in forest and along forest margins, compared with mixed scrub and open farmland. Camera trap deployment methods that increase detections, particularly of elusive carnivores, will add confidence to the effectiveness of future control operations.

6.1 Introduction

For wildlife management, population surveys are necessary to understand the distribution and relative abundance of a target species. Population survey areas are often too large for every individual of a population to be detected and counted (Royle & Nichols 2003; Stanley &

Royle 2005) and this inference is often flawed for cryptic species and those occurring at low densities (MacKenzie et al. 2002; Royle & Nichols 2003; MacKenzie 2005). Often the problem is low detection (i.e. the probability of an individual being detected is much less than one) and this problem has inspired a variety of different statistical models for estimating population abundance and dynamics (Dorazio & Royle 2005).

Another issue to account for in estimating population sizes is heterogeneity in detection probability at the individual monitoring station level (Royle & Nichols 2003; MacKenzie et al. 2004). Failure to adjust for heterogeneity in detection probabilities assumes constant abundance throughout the sites, which is also often incorrect (Royle & Nichols 2003; Tobler et al. 2015). Animals will usually be detected more easily where they are more abundant (Royle & Nichols 2003) and the detection probability may also vary as a function of the season, site heterogeneity (as in habitat complexity), animal behaviour, community structure, competitors/predators (Fancourt 2016; Allen et al. 2017) and other environmental factors (MacKenzie et al. 2002; Royle 2006). As such, accurate estimates of relative abundance require a thorough understanding of detection probability and site-level heterogeneity.

Existing methods for estimating abundance, such as capture-mark-recapture (CMR) through live trapping, and/or camera trap identification, have traditionally been costly in both labour and time, and they are also potentially inaccurate through human observation errors (Royle & Nichols 2003; Nichols et al. 2017b). More recently, some population models now incorporate spatial components to estimate population size (Chandler & Royle 2013; Royle et al. 2013). The spatial presence absence (SPA) model (Ramsey et al. 2015) is an extension of the spatial capture-recapture (SCR) model used by Chandler and Royle 2013) and estimates the relative abundance from detection/non-detection data. The SPA model is a Bayesian approach used previously with camera traps to estimate the population size of red foxes (*Vulpes vulpes*), although the model required relatively high numbers of detections to reliably converge (often an issue with predators occurring at low densities (Ramsey et al. 2015). The SPA model also allows non-independence of camera stations, assuming individuals can encounter multiple cameras within their normal home range (Ramsey et al. 2015). Another approach to estimate relative abundance, and the effect it has on detection probabilities, is the RN model (Royle & Nichols 2003; Bengsen 2014). The RN model extends the traditional occupancy model (MacKenzie et al. 2002) to account for heterogeneity among sites, sampling units, or other environmental factors (Royle & Nichols 2003).

6.1.1 Camera trap deployment

There are many variables to consider when deploying a monitoring device across a landscape, depending on the studies' target species, objectives, and intended statistical analyses. Carnivores often occur at low densities and have cryptic behaviour (Allen et al. 2017; Rich et al. 2017), which require sophisticated monitoring and statistical modelling techniques to circumvent the issue of low detection (Linden et al. 2017). Camera traps have become an increasingly popular tool for providing population estimates of a variety of carnivore species (Sarmento et al. 2009; Allen et al. 2017; Linden et al. 2017), including feral cats (Robley et al. 2010; Bengsen et al. 2011; Glen et al. 2016). Camera traps may be deployed in a variety of ways, such as with a horizontal or vertical orientation (Smith & Coulson 2012; Nichols et al. 2017a), and non-biased or biased allocation across a landscape (Meek et al. 2014a), as in systematic grids/transects (Gerber et al. 2012; Allen et al. 2017) or deliberately placed near target species 'hot spots', such as trails, roads, water features, etc. (Mann et al. 2015). Camera trap sites can baited (du Preez et al. 2014) and often there is wide variation in their deployment within a landscape (i.e. number of sampling units used at each site and their distance from each other) (Pebsworth & LaFleur 2014; Colyn et al. 2017).

6.1.2 Feral cats as a target species for monitoring

Feral cats are implicated in at least 14% of the world's mammal, reptile and bird extinctions (Medina et al. 2011; Doherty et al. 2015). Cats are adaptable and have variable home ranges (~1.3 km^2 for males, and 2 km^2 for females) that may overlap, depending on resource availability and population size (Langham & Porter 1991). Cats may prefer a variety of habitats, but most often those that include water sources and a mix of forest cover (both exotic and native), as well as open landscapes (Barratt 1997; McGregor et al. 2015). As a result, regular control operations are often in place to reduce the impacts of feral cats in New Zealand and Australia (Algar & Burrows 2004), and accurate and efficient monitoring is needed to measure effectiveness.

Chapter 4 used a spatially-correlated grid system of camera traps (~500 m spacing) to monitor feral cats in similar habitat to the current study. The main objective of Chapter 4 was to determine the accuracy and precision of the SPA model using detection/non-detection data to estimate changes in abundance, detection probability pre- and post- a predator control operation; as well as to compare to four other statistical models, IMI, CMR, and GLMM. What my Chapter 4 study indicated was that all the models struggled with low precision due to low detections; however, in particular, the SPA model (Ramsey et al. 2015) requires high

numbers of multiple detections to reliably converge (only ~1% detection probability, even using a lure).

In this current study, I aimed to increase the overall detection rate of feral cats by strategically placing camera traps in areas of high expected cat activity and with wider spacings than in Chapter 4 (i.e. camera traps will be independent of each other and may be analysed using non-spatial models; (O'Connell & Bailey 2011; Colyn et al. 2017). Again, I implemented the GLMM method, using a binomial distribution to calculate the rate of detection for feral cats at each site. I then compared the precision of the GLMM method with that of the RN model by Royle & Nichols (2003), which also estimates a rate of detection andrelative abundance, for each site. Although camera trap placement was strategic in that stations were placed in areas of high expected cat activity (i.e. forests and near forest margins), the required distance (~2 km) between camera traps meant not all stations could always be placed in preferred habitat type. Because of this, I also examined the effect habitat type had on detection probabilities.

6.2 Materials and methods

The study took place within the *Cape to City* programme in the Hawke's Bay, North Island, New Zealand (~39º S, 177º E; Fig. 1). The study area is a 26,000 ha portion of land with predefined areas destined for predator removal and other areas where no control will take place. I used two study sites, referred to as Site 1 (c. 18,000 ha where control work was designated to happen in the future), and an adjacent site, Site 2 (c. 8,000 ha which was going to be used as a no-control comparison site). Both sites had a similar mixture of rural and semi-urban habitats. The *Cape to City* programme is a large-scale, predator control project targeting feral cats, ferrets (*Mustela furo*) and stoats (*M. erminea*) and this study was intended to be the baseline monitoring operation.

In November 2015, I placed 38 camera traps (Browning Strike Force BTC-5, Prometheus Group, Birmingham, Alabama) in Site 1 and 30 in Site 2. Cameras in both areas were placed in either forest (both exotic and indigenous), forest margins (any edge between a forest and another habitat), open (exposed farmland), or mixed (scrub, rocky areas, or a combination of the above) habitats. The camera deployment strategy included a bias towards ideal 'predator habitat', such as near water sources, rock formations, forests and on any forest margins. Paddocks with large numbers of livestock, including red deer (*Cervus elaphus*), sheep (*Ovis aries*) and cattle (*Bos taurus*), were avoided to protect the cameras from damage and to reduce the number of non-target images, as previously experienced in Chapter 4.

Cameras were deployed for 21 days. Images were taken in bursts of three with a five second time lag between trigger events. All images were marked with a date/time stamp. The camera's field of view was positioned horizontally, parallel with the ground (10 cm from ground to the base of the camera (Chapter 4), set on brackets screwed into trees or wooden stakes and facing south, to avoid false triggers from the sun during the day. If necessary, vegetation was cleared from the camera's field of view (approximately 1 m wide and 2 m long directly in front of the camera) to reduce false triggers from vegetation moving (Kelly & Holub 2008), A perforated vial containing ferret odour (towels impregnated with the scent of a male ferret) was placed 1.5 m in front of all the cameras as a scent lure (Garvey et al. 2017) and secured with a tent peg to avoid removal by animals. Garvey *et al.* (2017) had previously performed a study simultaneously with the work from this thesis, which indicated that the apex predator odour was attractive for feral cats. All cameras were placed at ~2 km intervals, making them all independently spaced according to literature on feral cat home-ranges (Langham & Porter 1991).

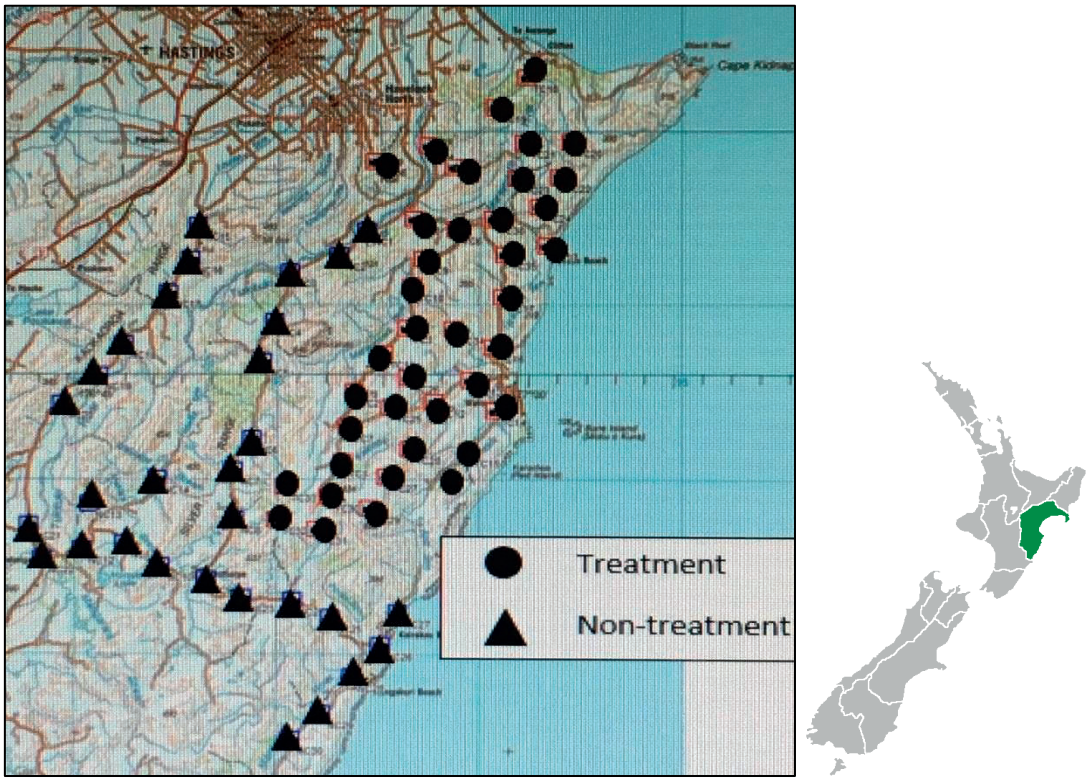


Figure 8 Location of camera trap stations across both study sites in Hawke's Bay, North Island, New Zealand 2015

Table 5 Numbers of camera stations (Sites 1 & 2 combined) per habitat type, and number of independent detection events for feral cats monitored in the Hawke's Bay, North Island, New Zealand, 2015

Habitat	Forest	Forest margin	Open	Mixed
Number of camera stations	24	16	9	16
Detections	60	38	2	13
Habitat	Forest	Forest margin	Open	Mixed
Number of camera stations	24	16	9	16

6.3 Data analysis

For both statistical models, I created daily detection histories for cats per camera trap night (as taken from midnight to midnight) denoted by either a '1' or a '0', respectively. I implemented the RN model with the detection histories for each combination of site and habitat type, to estimate the relative cat abundance at each camera station (Bengsen 2014). These estimates were then averaged over the entire survey period. Thus, the abundance estimates for this survey period represent the mean number of animals that were expected to have been detected by camera trap stations during the survey, whether or not they were actually detected (Bengsen 2014). This method specifically models differences in detection probability, thereby avoiding the problem of abundance being confounded with detectability, that is common in relative abundance indices (Bengsen 2014). The model allows heterogeneity (Bengsen 2014) at the camera station level, which influences the increases in precision at the overall site level. The following assumptions were made for both models: 1) the populations were deemed closed within the sampling period of 21 days; 2) camera trap stations were spatially independent of each other; and 3) detection events are independent of each other.

6.3.1 GLMM method

I used a GLMM with a binomial error distribution to estimate a rate of detection for all the cameras at each site. I originally analysed the numbers of multiple cat detections per night (as in an activity index with a Poisson error distribution); however, with very few detections, I found it more appropriate to use a binomial distribution. Camera station and night were

random effects, while site was a fixed effect. The model was fitted in R 3.2.4 (R Development Core Team 2016) using code from Bengsen et al. (2014) that produced separate indices for each site.

6.3.2 RN model

This model estimated a detection rate for cats at each site for the entire study period, as well as their relative abundance. The RN model followed a similar method to Bengsen's (2014), using the package 'unmarked' (Fiske & Chandler 2011) in R version 3.2.4 (R Development Core Team 2016). To estimate the effect of habitat type on detection probabilities and abundance, I classified each camera station as located in either forest (F), forest margin (Ma), mixed scrub (Mi), or open farmland (O). For this modelling, the global model allowed both detection rate and relative abundance to vary according to whether camera stations were located in the different sites or habitat types; whereas, for the null model, these remained constant.

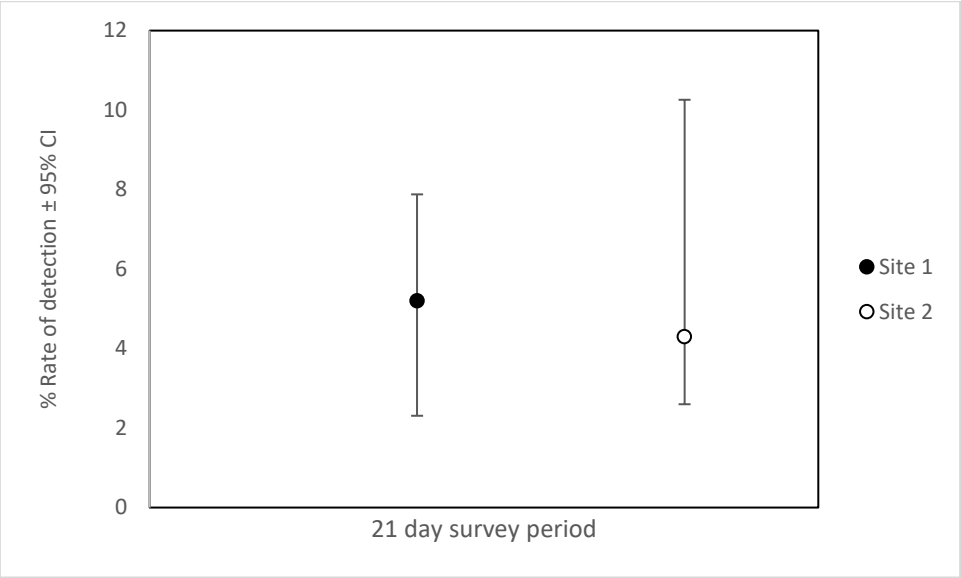
6.4 Results

6.4.1 Camera detection and habitat

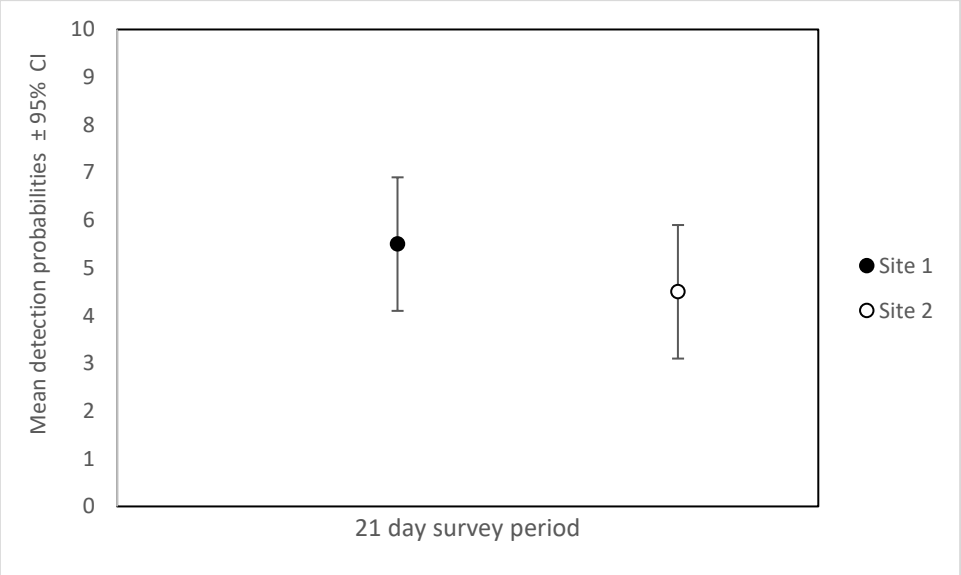
A total of 65 camera traps (out of 68) remained operative over a total of 1197 trap nights. Three cameras were removed due to malfunction/user error. There were 60 cat detections in forest habitat, 38 detections in forest margin, two detections in the open habitat, and 13 in mixed scrub (Table 5).

6.4.2 GLMM method

According to the GLM model, detection rates for cats were similar for both sites (P = 0.6) at 5.2% (95% CI 2.3-7.8) for Site 1 and 4.3% (2.6-10.3) for Site 2 (Fig. 9a).



a)



b)

Figure 9 a) Rate of detection for feral cats at each site (with 95% CI) estimated using the GLMM, b) Probability of detection for feral cats at each site (with 95% CI) estimated using the RN model

6.4.3 RN model

The RN modelling indicated little support for the global model (ΔAIC <2 from the null model) indicating that there was little evidence of differences in detection rates and abundance between the sites, with an estimated rate of detection for Site 1 of 5.5% (95% CI 4.1-6.9) and 4.5% (3.1- 4.9) for Site 2 (Fig 9b). The average relative abundance of cats was 12.6 (6.9-22.8) on site 1, and 8.3 (4.6-14.9) on site 2. Given that I was unable to detect any significant differences between the sites (see above) the data were pooled across both sites to

explore the effect of habitat type, due to relatively low numbers of cameras in some habitat types. This time the modelling indicated little support for the null model and indicted that detection rates varied according to habitat type but not abundance (ΔAIC = 4.11 from the null model; Fig. 10).

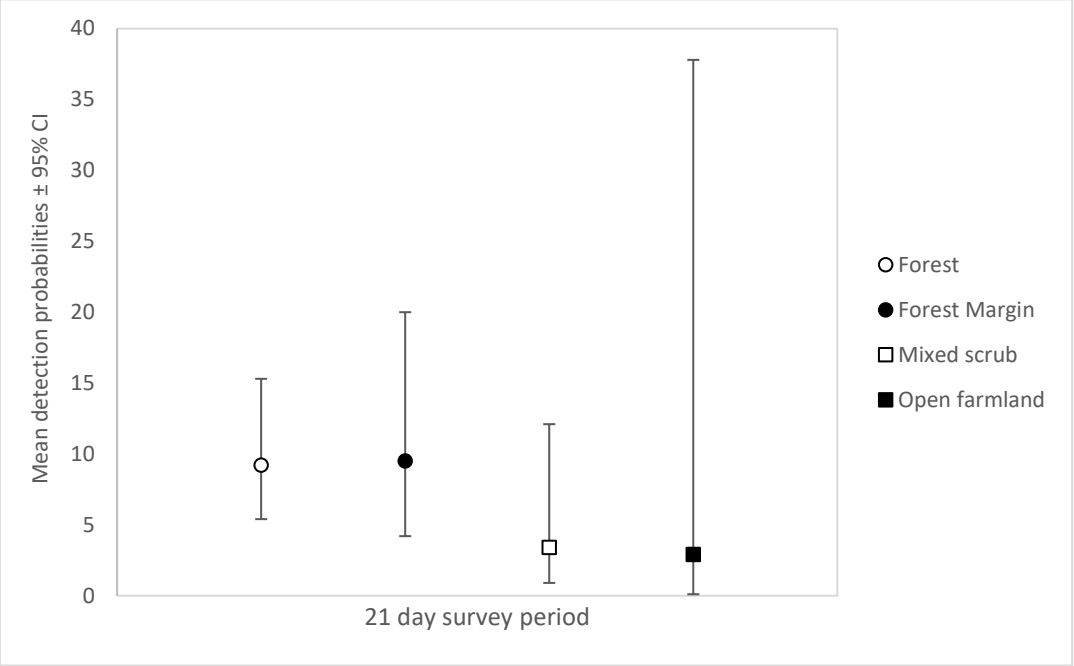


Figure 10 Detection probabilities for both sites combined (with 95% CI) by habitat type, using the RN model

Figure 11 Image of feral cat and combination lure vial

6.5 Discussion

As pest management operations extend to larger landscapes (e.g. Russel et al. 2015), the need for efficient, accurate, and precise monitoring increases. The primary goal of this study was to determine whether an alternative camera trap deployment strategy (i.e. with biased placement for feral cats) increased detection rates. The GLMM from Chapter 4 only estimated a detection rate of ~1% at the site pre-predator control (in a similar landscape and similar number of cameras, with the present study achieving detection rates of up to 5%. In addition, my assessment of the RN model showed a significant variation in detection due to habitat; thus, heterogeneity should be taken into account.

Both the GLMM and RN model showed little difference in cat detections and relative abundance for the two sites. Both sites were similar in habitats, however, Site 1 was substantially larger in size than Site 2, thus slightly fewer cameras could be used at Site 2. At both sites, cat detections were similar among the forest and forest edges, but much higher than in the mixed scrub and open farmland habitats. The estimate for open farmland did have low precision mainly due to a low number of sampling units using this habitat type (Fig. 10) and so assumptions based on this result should be treated with some caution. When explaining the preference for forest and forest edges it is likely that cats preferred the cover provided by these habitats, as stated in a review by Doherty *et al.* (2014). This may also be in accordance with habitat selection of prey populations, such as rabbits (*Oryctolagus cuniculus;* (Recio & Seddon 2013). Accordingly, we recommend in future studies that cameras should be placed in forest or forest edge habitats whenever possible for detecting feral cats.

Summary of optimal monitoring and statistical modelling methods for feral cats and other predators in a pastoral landscape

Chapter 7

7.1 Summary of results

In Chapter 3, I found horizontal placement of camera traps captured significantly more photos of the target species, a higher number of species overall (both target and non-target), and more encounters with the target species. Although false triggers were more common among cameras placed horizontally, the difference was not statistically significant.

In Chapter 4, the IMI method, SPA model, and GLMM method all showed a similar decrease in cat abundance and detections post-predator control. However, the CMR method was unable to converge?? due to the low sample size of identifiable images of cats. Upcoming species recognition software may remedy this issue in the future. The IMI method was a highly reliable estimate and was relatively simple to implement using a variance formula, however requires two population measurements. The GLMM method and SPA model estimated a similar decrease in cat detection rates and abundance post-predator control; however, the SPA lacked precision, and struggled to converge when multiple detections were low. The GLMM method is a reliable estimator when dramatic changes in a population occur, as in the current study. However, detection rates were extremely low throughout and strategies were undertaken in Chapter 6 to increase numbers of detections.

In Chapter 5, the SPA model was applied to estimate hedgehog abundance using the same camera trap array as seen earlier in this thesis. Many studies have examined hedgehog home ranges; however, few have estimated hedgehog abundance, particularly in New Zealand. The SPA model performed well when applied to a data set of higher detections, as in a population of hedgehogs. Hedgehog abundance was reduced by 60% during the three-week period. The SPA model has shown to be a useful tool to estimate the effectiveness of a control operation, especially for hedgehogs.

In Chapter 6, the large scale ecological restoration project, *Cape to City,* was the site of my final study. Here, I placed cameras independently (~2 km) and in favour of preferable cat habitats. Once again, I implemented the GLMM method to to examine any differences in detection rates between two sites destined for predator control. I also used the RN model to

estimate detection probabilities and relative abunance at the two sites, including the effect of habitat on feral cat detection probabilities.

In conclusion, camera trap data may be analysed in various ways to estimate the presence or abundance of a target species. The IMI method, while more traditional, and requiring two measures of a population, was very accurate, simple to estimate and, perhaps, of value when a known number of animals were removed during future control operations. While the SPA model was able to estimate animal abundance on a localised scale of a few square kilometres, it required intensive sampling, and may not be appropriate for cryptic species that occur at low abundance. However, it is important to note that the estimates from both the IMI and SPA model were incredibly similar; thus, we can assume some amount of precision for the IMI method. The GLMM method can withstand/manage?? low detections and was the simplest method to implement. However, this method may be reserved for large shifts in population size, having less precision that the RN model. The RN model seemed to be the most versatile and precise statistical model for this selection of data.

Future research

It would be useful to repeat the camera orientation study (Chapter 3) in a pen trial scenario with an increased height for the vertical camera. This would increase the size of the camera's field of view, potentially increasing detection probabilities for cats and other predators. In addition, coat patterns may be more easily identified from above (Hohnen et al. 2013) increasing the ability to identify individuals.

A major goal for future research is to increase the bdetection rates. There may be several reasons for the low detection rates in Chapter 4. Also, the device spacing may not be appropriate for the target species when at low densities. Recent research suggests that using multiple cameras can increase detections (Mann et al. 2015; Stokeld et al. 2016). Based on this complementary research, I recommend further camera trapping trials use independently spaced cameras (>2 km apart for feral cats in pastoral landscapes) and their deliberate deployment in attractive habitat to increase detection probabilities. Future research could examine optimal trap spacing and deployment design by statistically removing camera trap stations to leave a hollow grid (Efford et al. 2005) and also, possibly, use a cluster formation (Stokeld et al. 2016) of cameras available to detect feral cats. In addition, researchers could attempt to re-apply the SPA model with feral cats by incorporating information on the identity of individual animals (see: Ramsey et al. 2015) and placing camera trap stations in more favourable habitats.

Camera traps have shown an impressive ability to monitor a wide range of species over variable landscapes. Although, initially, more expensive than many other monitoring techniques, the information potentially derived from camera trap data is proving of great value, with a highly reduced labour expenditure. As with all technology, camera traps are rapidly changing, and newer, cheaper, and more effective models are produced almost annually/yearly??. Optimal, repeatable camera trap deployment strategies are necessary in order to standardise camera trapping as a successful monitoring technique. We also need to be aware of how accessible this technology has become and, although incredibly useful, there is still a long way to go in optimally processing these volumes of data and information.

Feral cats and other mammalian predators are inherently difficult to monitor and manage. This research will be useful not only for future predator monitoring in pastoral landscapes but is also highly applicable to other species that may be cryptic or occur at low densities. While there has been a great amount of research into the subject of both invasive mammalian predator distribution, and monitoring methods; this study has filled gaps in knowledge surrounding/about?? both subjects.

Appendices

Appendix A

A comparison of horizontal versus vertical camera placement to detect feral cats and mustelids

Margaret Nichols[1*], Alistair S. Glen[2], Patrick Garvey[3] and James Ross[1]

[1]Centre for Wildlife Management and Conservation, Lincoln University, Canterbury, New Zealand

[2]Landcare Research, Private Bag 92170, Auckland 1142, New Zealand

[3]School of Biological Science, Tamaki campus, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand

[*]Author for correspondence (Email: Maggie.Nichols@lincolnuni.ac.nz)

Abstract

Invasive predators are a threat to biodiversity in New Zealand. However, they are often difficult to monitor because of the animals' cryptic, mobile behaviour and low densities. Camera traps are increasingly being used to monitor wildlife, but until recently have been used mainly for large species. We aimed to determine the optimal camera alignment (horizontal or vertical) for detecting feral cats (*Felis catus*) and mustelids (*Mustela furo*, *M. erminea* and *M. nivalis*). We deployed 20 pairs of cameras, each pair with one horizontal and one vertical camera. We compared the number of photos of target species, non-target species, and false triggers (i.e. camera triggered with no animal present) between camera orientations. Horizontally oriented cameras captured approximately 1.5 times as many images of the target species compared with vertically oriented cameras, and also detected more non-target animals. Orientation did not have a significant effect on the number of false triggers.

Keywords: camera trapping; feral ferret; invasive species; *Mustela* spp.; stoat

Introduction

Invasive mammalian predators are among the greatest threats to New Zealand's biodiversity (Krull et al. 2015), but can be difficult to monitor due to their highly cryptic nature, and in some cases (i.e. feral cats) low densities (Glen et al. 2013). In recent decades, various methods have been used to assess mammal abundance and distribution, including trapping, hair snags, spotlight counts, scat

surveys, camera traps and tracking tunnels (Gompper et al. 2006; Long et al. 2007a, b; Pickerell et al. 2014; Lazenby et al. 2015). In New Zealand, tracking tunnels have been the most commonly used non-lethal method for monitoring small mammals such as rodents and mustelids (King & Edgar 1977; Brown et al. 1996). Although there are indeed many successful monitoring methods available for small to medium-sized mammals, over the last 20 years attention has turned towards camera traps as an effective research tool (Rowcliffe & Carbone 2008). Since camera traps are remotely triggered and impervious to most weather conditions, they may be left for long periods of time for monitoring purposes (Long et al. 2007a; Meek et al. 2014a). Camera traps may also have higher detection rates than some other monitoring techniques such as tracking tunnels and live capture traps (Sam 2011), and have the potential to identify uniquely marked individuals (Heilbrun et al. 2003; Long et al. 2007a, b; Sam 2011).

Numerous studies have used camera traps for large mammals such as leopard (*Uncia uncia*), jaguar (*Panthera onca*) and tiger (*Panthera tigris*) (Karanth et al. 2004; Jackson et al. 2006; Kelly et al. 2008; Tobler et al. 2008; Wang & Macdonald 2009), but only a handful have examined the optimal specifications for small to medium-sized species (e.g. De Bondi et al. 2010; Glen et al. 2013; Bischof et al. 2014). There is a wide range of variables associated with camera traps, from trigger settings to sensor types as well as data analysis methods (De Bondi et al. 2010; Meek et al. 2014a). Additionally, camera orientation, along with height from the ground, detection zone, distance from a lure (if used), and the size of the target species must all be considered when deploying camera traps (Smith & Coulson 2012; Glen et al. 2013; Taylor et al. 2013; Meek et al. 2014a). Camera traps are usually oriented horizontally at a height to accommodate the size of the target species (Smith & Coulson 2012). De Bondi et al. (2010) tested an alternative approach by placing cameras vertically, angled at 90 degrees facing towards the ground to capture photos from above the target – a technique now known as vertical orientation (Smith & Coulson 2012). This method has the advantage of standardising the size of the camera's detection zone, but orientation may also affect the success of certain camera traps in detecting animals that encounter the traps.

Smith and Coulson (2012) compared vertical and horizontal orientation for two Australian marsupials, potoroos (*Potorous tridactylus*, 660–1640 g; Norton et al. 2011) and bandicoots (*Isoodon obesulus*, >1 kg; De Milliano et al. 2016). They found that vertically oriented cameras had a detection probability for these target species up to five times greater than horizontal cameras. Taylor et al. (2013) performed a similar study with bandicoots, potoroos and pademelons (*Thylogale stigmatica*, 4–7 kg; Macqueen et al. 2009). However, this study found horizontally oriented cameras had detection probabilities 2.5 times greater than vertically oriented cameras. These studies varied in both deployment and set-up methods.

We aimed to compare the effectiveness of horizontal and vertical camera trap orientations for detecting feral cats (*Felis catus*) and mustelids (feral ferrets *Mustela furo*, stoats *M. erminea* and weasels *M. nivalis*). Like the marsupials mentioned above, these species range in size, with typical cats weighing 1–5 kg, ferrets 600–1200 g, stoats 200–325 g and weasels 55–125 g (King 2005). We

compared the number of photos of target species between cameras with these two orientations, along with the number of false triggers (when cameras were triggered without capturing an image of an animal), the total number of photos taken throughout the study (including target species, non-target species and false triggers), and the number of independent encounters (Brook et al. 2012) with individuals of the target species (as distinct from repeated images of the same animal).

Methods

Study area and field methods

The study was conducted on Toronui Station, a pastoral property in Hawke's Bay, North Island, New Zealand (39°0' S, 176°46' E). Toronui Station (1600 ha) is mainly covered by introduced pasture grass, with fragments of native beech forest (*Fuscospora solandri*), on both high country and lowland paddocks (300–1000 m above sea level). Fence lines were often hedged with pines (*Pinus radiata*) as windbreaks for livestock, which included red deer (*Cervus elaphus*), sheep (*Ovis aries*) and cattle (*Bos taurus*).

From 20 January to 24 March 2014, 20 pairs of cameras were placed along existing monitoring transects. Paired camera trap sites were spaced 2.4 km apart on average, with a minimum separation of 700 m. We placed cameras at the ecotones of forest fragments wherever possible, to increase predator detection rates (Meek et al. 2014a). Two cameras were placed 1.5 m apart at each station. One camera was placed on a steel fence post facing vertically towards the ground from a height of 1.5 m. The other was set horizontally, 7 cm from the ground (as measured to the base of the camera) and attached to a tree or wooden stake (Fig. 1). As part of a concurrent trial, European rabbit meat (*Oryctolagus cuniculus*) and ferret odour (towel bedding from a male ferret's enclosure) lures were separately contained in two perforated vials, and set directly beneath the vertical-facing camera. This design allowed the lure vials to be within the field of view of both cameras.

We primarily used Reconyx Hyperfire PC900 trail cameras (Reconyx Inc., Holmen, Wisconsin, USA), but also LTL Acorn 5210A (Shenzen LTL Acorn Electronics Co., Ltd, Shenzen, Guangdong, China), M990i (Moultrie, Calera, Alabama, USA) and Bushnell (Bushnell Outdoor Products, Overland Park, Kansas, USA) (see Table 1 for camera types, specifications and settings). All cameras were chosen for their infrared flash, which is likely to be less conspicuous to cats than a white flash (Glen et al. 2013; but see also Meek et al. 2014b). Vegetation was cleared to a height of 5 cm where necessary to provide a clear view of animals in the detection zone and to avoid possible false triggers caused by moving branches or foliage (Kelly & Holub 2008; Taylor et al. 2013). Cameras were checked after 4 weeks, and batteries, memory cards (4–8 GB) and scent lures were replaced. Photos were uploaded onto an external hard drive according to their site number and orientation. All photographed animals were recorded in an Excel™ file along with any false triggers, following the methods of Allen (2014).

Figure 1 Setup of horizontal and vertical cameras, Toronui Station, New Zealand, in 2014. Reconyx cameras are shown below; camera models and settings are given in Table 1.

Table 1 Camera specifications and settings used at Toronui Station, New Zealand, in 2014

	Camera type			
	Reconyx ®	**LTL Acorn ®**	**Moultrie ®**	**Bushnell ®**
Trigger speed (seconds)	0.2	0.8	0.69	0.2
Recovery time (seconds)	0.5	1	5	1
Flash range (metres)	15	15	15	24
Sensor	PIR	PIR	PIR	PIR
Light source	Infrared flash	Infrared flash	Infrared flash	Infrared flash
Sense level (normal, high, low)	Normal	Normal	Normal	Normal
Number of photos per trigger	3	3	3	3
Number of cameras	24	10	4	2

Data analysis

Photographs were classed as either: (1) target species, (2) non-target species, or (3) false trigger events. To increase the sample size, we pooled cats and mustelids for analysis simply as 'target species'. We plotted histograms of the elapsed time between successive photographs of the target species to isolate encounters with an individual animal from repeated observations of the same individual (Brook et al. 2012). The average time between consecutive photographs of cats was <10 minutes, indicating these to be repeat detections. Therefore, we assumed photographs taken >30 minutes apart were 'independent encounters' representing separate individuals, except for individuals that could be identified reliably (e.g. by coat pattern). Similarly, on the basis of the activity patterns of mustelids, (consecutive photographs <5 minutes apart) we assumed encounters >15 minutes apart were independent.

We used the software program GENSTAT version 15 (VSN International 2011) to create generalised linear mixed-effects models. A Poisson error distribution was used as we had continuous count data. To assess the performance of the two camera orientations at capturing target species, camera orientation (vertical or horizontal) was fitted as a fixed effect, and camera type and the camera monitoring stations were random effects. We used likelihood ratio tests to compare models with each of four response variables (numbers of target species photos, independent encounters with target species, all photos and false triggers) to the corresponding null model without an orientation parameter.

Results

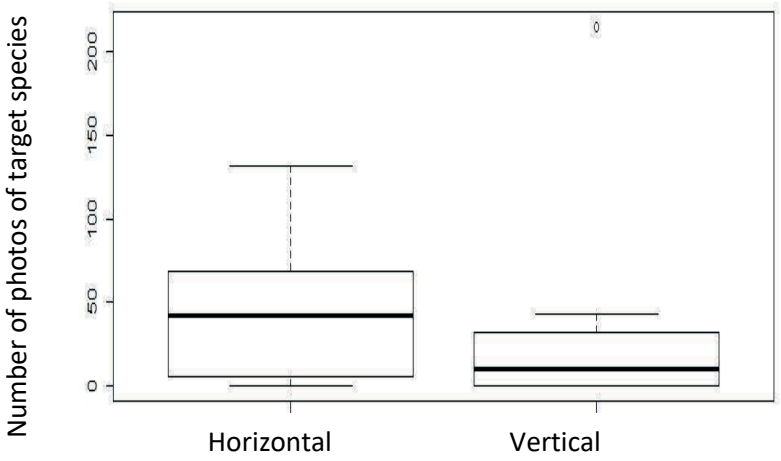
Data from 36 of the original 40 cameras were used. One camera was damaged by livestock, one was damaged by flooding and two cameras had memory cards filled to capacity, due to false triggers and livestock. The cameras detected 79 independent encounters with cats (50 on the horizontal cameras and 29 on vertical cameras), 45 independent encounters with stoats (25 horizontal and 20 vertical), and two independent encounters with ferrets (horizontal only). There were also 23 independent encounters with target species that were detected by both camera orientations. No weasels were detected. Non-target species (83% of all photos taken) included house mouse (*Mus musculus*), ship rat (*Rattus rattus*), Norway rat (*R. norvegicus*), brushtail possum (*Trichosurus vulpecula*), European hedgehog (*Erinaceus europaeus occidentalis*), European rabbit, feral pig (*Sus scrofa*), Eurasian blackbird (*Turdus merula*), house sparrow (*Passer domesticus*) and silvereye (*Zosterops lateralis*).

Table 2 Number of photos of target and non-target species, and false trigger events obtained from cameras with horizontal and vertical alignment, at Toronui Station, New Zealand, in 2014

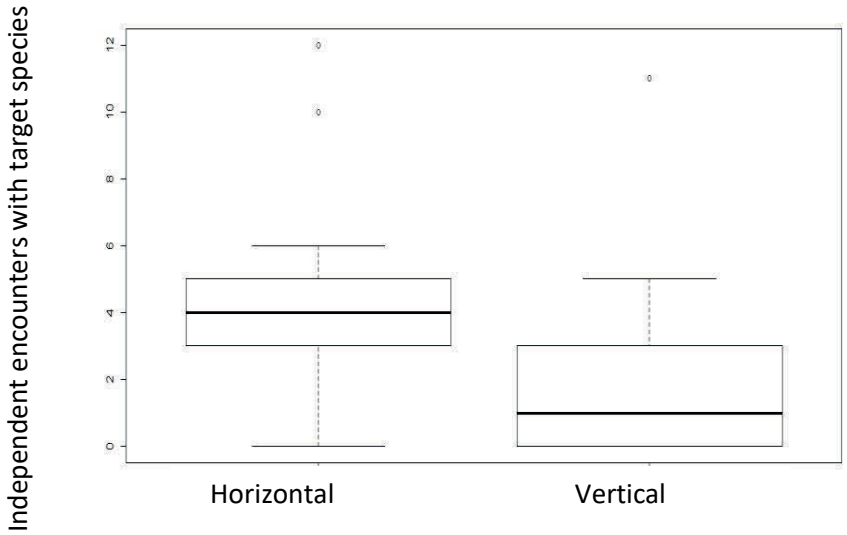
Orientation	Target species (stoats, ferrets, cats)	Non-target species	False triggers	Total photos
Horizontal	832	22117	3746	26695
Vertical	571	11478	2013	14062

Horizontally oriented cameras yielded significantly more photos of target species compared with vertical cameras ($\chi^2 = 4.54$, d.f. = 1, 15, $P = 0.05$) (Table 2; Fig. 2a). Horizontally placed cameras also captured significantly more independent encounters with target species than did the vertical cameras ($\chi^2 = 5.55$, d.f. = 1, 15.4, $P = 0.032$) (Fig. 2b), and significantly more photos in total (false triggers, target and non-target species) ($\chi^2 = 15.67$, d.f. = 1, 22.1, $P = 0.001$) (Table 2; Fig. 2c). However, orientation did not significantly affect the number of false triggers ($\chi^2 = 0.41$, d.f. = 1, 16.7, $P = 0.53$) (Table 2; Fig. 2d). Vertical cameras often provided clearer images than horizontal cameras of the coat patterns of cats. However, the large body size of cats relative to the camera's field of view meant that 63% of cats photographed by vertical cameras were partially outside the frame. The corresponding proportion for horizontal cameras was 36%.

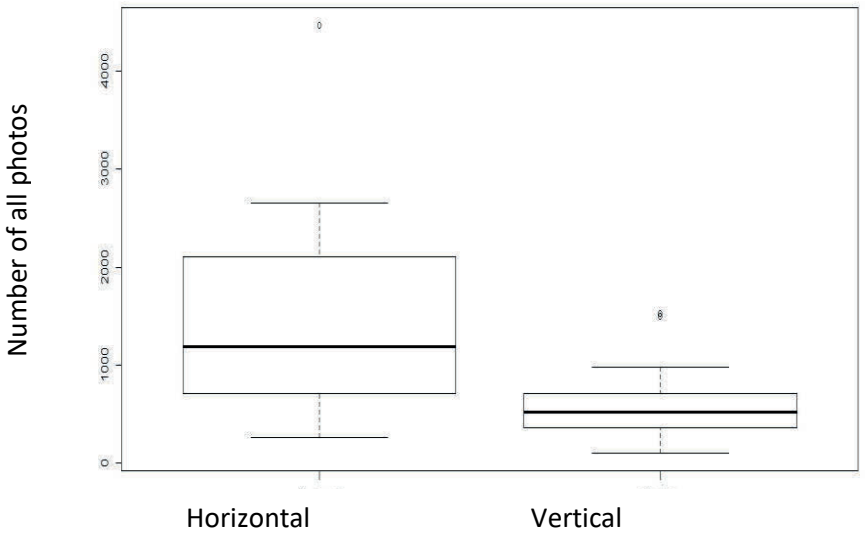
a)



b)


Independent encounters with target species
0
2
4
6
8
10
12
Horizontal
Vertical

c)


Number of all photos
0
1000
2000
3000
4000
Horizontal
Vertical

d)

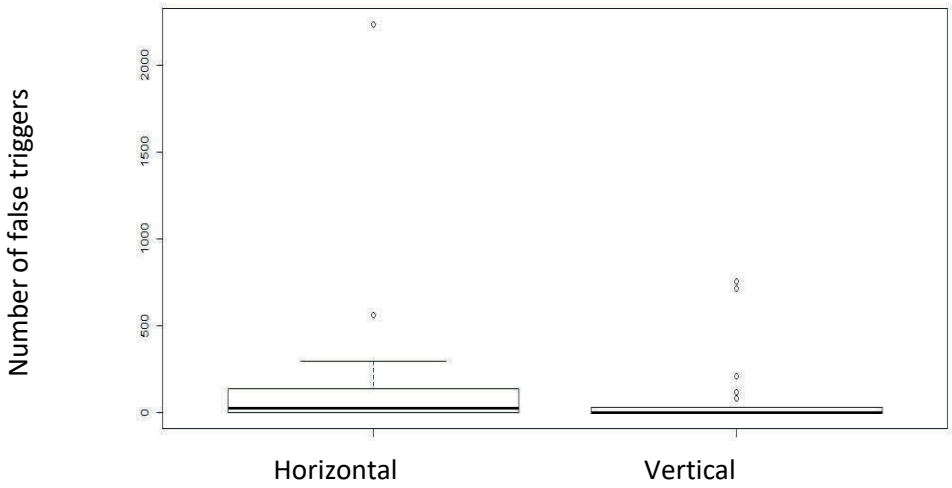


Figure 2 Number of photos of target species, (b) independent encounters with a target species, (c) total photos over all, and (d) false triggers by cameras with horizontal and vertical alignment. Camera models and settings are given in Table 1.

Discussion

Our results showed that horizontally placed cameras were more effective at detecting the target species, i.e. cats and mustelids combined. Smith and Coulson (2012) found that the wider field of view associated with the horizontal cameras decreased detection rates for small to medium-sized species. There were differences in camera set-up including distance from the horizontal camera to the lure (3 m, 2 m, and 1.5 m respectively). There was also a difference in camera settings (i.e. continuous triggering (Smith & Coulson 2012) vs bursts of three images with a forced delay (Taylor et al. 2013).

There has been some debate over the optimal camera trap orientation for identifying individuals of a species (Smith & Coulson 2012; Taylor et al. 2013). De Bondi et al. (2010) observed that vertical cameras assisted in the species identification of mammals (smaller than cats) that fitted entirely in a camera's field of view. In contrast, although we found that cats' coat patterns were clearest in photographs taken directly beneath vertical cameras, full coat identifications would potentially have been difficult because the cats were often only partially in the fields of view of the vertical cameras.

In conclusion, our study shows that horizontal cameras are likely to detect more cats and mustelids than vertical cameras mounted at 1.5 m. However, should a study's aim be to identify individuals through coat patterns, further investigation into the utility of vertical camera orientation may be necessary. While vertical cameras may help identify animals, cameras must have a sufficiently wide field of view to capture complete images of the target species. Future studies could test vertical cameras raised >1.5 m from the ground to broaden the field of view and compensate for the larger size of feral cats, to improve coat identification.

Acknowledgements

This study was funded by the Hawke's Bay Regional Council and by core funding to Landcare Research from the Ministry of Business, Innovation and Employment. Many thanks to R. Dickson and S. Cave for their technical support and to D. Shaw for site access to Toronui Station. We also greatly appreciate the helpful comments from Deb Wilson and two anonymous reviewers on a previous version of the manuscript.

References

Allen B 2014. How to collect, store and query pest animal data: a tutorial for practitioners. In: Gentle M ed. Program and abstracts 16th Australasian Vertebrate Pest Conference, Brisbane. Pp. 87.

Bischof R, Ali H, Kabir M, Hameed S, Nawaz M 2014. Being the underdog: an elusive small carnivore uses space with prey and time without enemies. Journal of Zoology 219: 40–48.

Brook LA, Johnson CN, Ritchie EG 2012. Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. Journal of Applied Ecology 49: 1278–1286.

Brown K, Moller H, Innes J, Alterio N 1996. Calibration of tunnel tracking rates to estimate relative abundance of ship rats (*Rattus rattus*) and mice (*Mus musculus*) in a New Zealand forest. New Zealand Journal of Ecology 20: 271–275.

De Bondi N, White JG, Stevens M, Cooke R 2010. A comparison of the effectiveness of camera trapping and live trapping for sampling terrestrial small-mammal communities. Wildlife Research 37: 456–465.

De Milliano J, Di Stefano J, Courtney P, Temple-Smith P, Coulson G 2016. Soft-release versus hard-release for reintroduction of an endangered species: an experimental comparison using eastern barred bandicoots (*Perameles gunnii*). Wildlife Research 43: 1–12.

Glen AS, Cockburn S, Nichols M, Ekanayake J, Warburton B 2013. Optimising camera traps for monitoring small mammals. PloS one 8(6): e67940.

Gompper ME, Kays RW, Ray JC, Lapoint SD, Bogan DA, Cryan JR 2006. A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. Wildlife Society Bulletin 34: 1142–1151.

Heilbrun RD, Silvy NJ, Tewes ME, Peterson MJ 2003. Using automatically triggered cameras to individually identify bobcats. Wildlife Society Bulletin: 748–755.

Jackson RM, Roe JD, Wangchuk R, Hunter DO 2006. Estimating snow leopard population abundance using photography and capture-recapture techniques. Wildlife Society Bulletin 34: 772–781.

Karanth KU, Chundawat RS, Nichols JD, Kumar NS 2004. Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture–recapture sampling. Animal Conservation 7: 285–290.

Kelly MJ, Holub EL 2008. Camera trapping of carnivores: trap success among camera types and across species, and habitat selection by species, on Salt Pond Mountain, Giles County, Virginia. Northeastern Naturalist 15: 249–262.

Kelly MJ, Noss AJ, Di Bitetti MS, Maffei L, Arispe RL, Paviolo A, De Angelo CD, Di Blanco YE 2008. Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, and Belize. Journal of Mammalogy 89: 408–418.

King CM 2005. The handbook of New Zealand mammals. 2nd edn. Melbourne, Oxford University Press. Pp. 261–309.

King CM, Edgar R 1977. Techniques for trapping and tracking stoats (*Mustela erminea*); a review, and a new system. New Zealand Journal of Zoology 4: 193–212.

Krull C, Galbraith JA, Glen AS, Nathan HW 2015. Invasive vertebrates in Australia and New Zealand. In: Stow A, MacLean N, Holwell GI eds. Austral ark: the state of wildlife in Australia and New Zealand. Cambridge, Cambridge University Press. Pp. 197–226.

Lazenby, B. T., Mooney, N. J., & Dickman, C. R 2015. Effects of low-level culling of feral cats in open populations: a case study from the forests of southern Tasmania. *Wildlife Research*, *41*(5): 407-420.

Long RA, Donovan TM, Mackay P, Zielinski WJ, Buzas JS 2007a. Comparing scat detection dogs, cameras, and hair snares for surveying carnivores. Journal of Wildlife Management 71: 2018–2025.

Long RA, Donovan TM, Mackay P, Zielinski WJ, Buzas JS 2007b. Effectiveness of scat detection dogs for detecting forest carnivores. Journal of Wildlife Management 71: 2007–2017.

Macqueen P, Goldizen AW, Seddon JM 2009. Response of a southern temperate marsupial, the Tasmanian pademelon (*Thylogale billardierii*), to historical and contemporary forest fragmentation. Molecular ecology 18: 3291–3306.

Meek P, Ballard G, Claridge A, Kays R, Moseby K, O'Brien T, O'Connell A, Sanderson J, Swann D, Tobler M 2014a. Recommended guiding principles for reporting on camera trapping research. Biodiversity and Conservation 23: 2321–2343.

Meek PD, Ballard G-A, Fleming PJ, Schaefer M, Williams W, Falzon G 2014b. Camera traps can be heard and seen by animals. PloS one 9: e110832.

Norton MA, Claridge AW, French K, Prentice A 2011. Population biology of the long-nosed potoroo (*Potorous tridactylus*) in the Southern Highlands of New South Wales. Australian Journal of Zoology 58: 362–368.

Pickerell GA, O'Donnell CF, Wilson DJ, Seddon PJ 2014. How can we detect introduced mammalian predators in non-forest habitats? A comparison of techniques. New Zealand Journal of Ecology 38: 86–102.

Rowcliffe JM, Carbone C 2008. Surveys using camera traps: are we looking to a brighter future? Animal Conservation 11: 185–186.

Sam S 2011. New monitoring and control tools for simultaneously managing possums, rats and mice in New Zealand. Unpublished PhD thesis, Lincoln, Lincoln University: 1-149

Smith JK, Coulson G 2012. A comparison of vertical and horizontal camera trap orientations for detection of potoroos and bandicoots. Australian Mammalogy 34: 196–201.

Taylor BD, Goldingay RL, Lindsay JM 2013. Horizontal or vertical? Camera trap orientations and recording modes for detecting potoroos, bandicoots and pademelons. Australian Mammalogy 36: 60–66.

Tobler MW, Carrillo-Percastegui SE, Leite Pitman R, Mares R, Powell G 2008. An evaluation of camera traps for inventorying large-and medium-sized terrestrial rainforest mammals. Animal Conservation 11: 169–178.

VSN International 2011. GenStat for Windows. 14th edn. Hemel Hempstead, UK, VSN International.

Wang SW, Macdonald DW 2009. The use of camera traps for estimating tiger and leopard populations in the high altitude mountains of Bhutan. Biological Conservation 142: 606–613.

Editorial board member: Deb Wilson

Received 20 April 2016; accepted 15 August 2016

Appendix B

Exploiting interspecific olfactory communication to monitor predators

Ecological Applications, 27(2), 2017, pp. 389–402

Exploiting interspecific olfactory communication to monitor predators

Patrick M. Garvey,[1,2] Alistair s. Glen,[2] Mick N. Clout,[1] Sarah V. Wyse,[1,3] Margaret Nichols,[4] and Roger P Pech[5]

[1]*Centre for Biodiversity and Biosecurity, School of Biological Sciences, University of Auckland, Auckland, New Zealand*

[2]*Landcare Research, Private Bag 92170, Auckland, 1142 New Zealand*

[3]*Royal Botanic Gardens Kew, Wakehurst Place, RH17 6TN United Kingdom*

[4]*Centre for Wildlife Management and Conservation, Lincoln University, Canterbury, New Zealand*

[5]*Landcare Research, PO Box 69040, Lincoln, 7640 New Zealand*

Abstract. Olfaction is the primary sense of many mammals and subordinate predators use this sense to detect dominant species, thereby reducing the risk of an encounter and facilitating coexistence. Chemical signals can act as repellents or attractants and may therefore have applications for wildlife management. We devised a field experiment to investigate whether dominant predator (ferret *Mustela furo*) body odor would alter the behavior of three common mesopredators: stoats (*Mustela erminea*), hedgehogs (*Erinaceus europaeus*), and ship rats (*Rattus rattus*). We predicted that apex predator odor would lead to increased detections, and our results support this hypothesis as predator kairomones (interspecific olfactory messages that benefit the receiver) provoked "eavesdropping" behavior by mesopredators. Stoats exhibited the most pronounced responses, with kairomones significantly increasing the number of observations and the time spent at a site, so that their occupancy estimates changed from rare to widespread. Behavioral responses to predator odors can therefore be exploited for conservation and this avenue of research has not yet been extensively explored. A long-l ife lure derived from apex predator kairomones could have practical value, especially when there are plentiful resources that reduce the efficiency of food-b ased lures. Our

results have application for pest management in New Zealand and the technique of using kairomones to monitor predators could have applications for conservation efforts worldwide.

Key words: carnivore; conservation behavior; eavesdropping; interference competition; invasive species; monitoring; olfaction; pest management; pheromone; predator odor.

Introduction

Apex predators shape and drive community structure, either directly through agonistic encounters or indirectly as mesopredators alter their behavior in response to predation risk (Ritchie and Johnson 2009). Natural selection will encourage the development of mechanisms for subordinate species to recognize dominant predators and avoid confrontations (Kats and Dill 1998, Monclús et al. 2005). Olfaction, the primary foraging sense of most mammals, may mediate trophic interactions by allowing subordinate species to assess the risk of encounter (Roberts and Gosling 2001). Predators deposit odor into the environment, either unintentionally as by- products of metabolic processes or deliberately for communication (Ferrari and Chivers 2009, Wyatt 2010). In this context, communication is deemed to occur when the cues given by one individual influence the behavior of another (Wiley 1983). Odor signals, termed "kairomones" when intercepted by eavesdropping sympatric species, are primarily produced for intraspecific communication and provide the receiver with information on the depositing species (Peake 2005, Ferrari and Chivers 2009). For example, temporal variation in scent quality can indicate the time elapsed since an odor was deposited (Bytheway et al. 2013) or odor can facilitate predator identification, which may then be related to the risk of encountering this predator (Schoeppner and Relyea 2009). Kairomones may additionally supply information that can help inform the foraging decisions of the eavesdropping species (van Dijk et al. 2008). Unlike visual or auditory cues, odor deposits indicate that a location was risky at some point in the past, but this may not relate to present risk (Kats and Dill 1998). Therefore, odors can be ambiguous and require careful inspection to elicit all the information contained in a scent (Hemmi and Pfeil 2010).

Mammalian chemical communication has been exploited for a range of wildlife management applications: to reduce human-w ildlife conflicts, improve population monitoring, influence habitat selection,

reduce predation, increase the welfare of captive animals, encourage captive breeding, and to improve the success of release programs (Campbell-P almer and Rosell 2011). Olfactory attractants are primarily food

389

Manuscript received 19 May 2016; revised 11 September 2016; accepted 8 November 2016.
Corresponding Editor: Aaron J. Wirsing.

[6]E-mail: pgar874@aucklanduni.ac.nz

based, but occasionally non- prey pheromone lures such as beaver (*Castor canadensis*) castoreum or muskrat (*Ondatra zibethicus*) scent glands are deployed to attract target species (Long et al. 2012). Intraspecific (pheromone) lures, that stimulate territorial or social responses in conspecifics, have been deployed for wildlife management; for example, lures derived from the scent gland of culled American mink (*Mustela vison*), an alien species in Europe, were used to attract conspecifics to traps and proved as successful as a food based lure during control operations (Roy et al. 2006). Interactions between predators and prey have also been exploited to create deterrents, as predator odor may induce avoidance behaviors, reducing foraging damage by prey species (Apfelbach et al. 2005). Lures have yet to be developed that exploit interspecific olfactory communication between predators.

New Zealand has one of the highest proportions of threatened taxa in the world, a trend primarily driven by introduced invasive species (Clout 2001, Towns et al. 2006). Island faunas are particularly vulnerable to extinction (McKinney 1997), as many species evolved in the absence of mammals and therefore lack appropriate defensive mechanisms to avoid predation (Terborgh 1974). New Zealand's mammalian carnivores were introduced in the hope that they would act as biological control agents for pests such as rabbits (*Oryctolagus cuniculus*) but, as generalist predators, they attack vulnerable native species as well as introduced mammals (Wodzicki 1950, King and Powell 2007, Wallach et al. 2015). Trophic interactions also occur within this novel invasive predator guild, influencing behavior through interference competition, which will in turn cascade to lower trophic levels (Garvey et al. 2015). Since sympatric predator odor is likely to provoke a response in these mesopredators there may be an opportunity to exploit eavesdropping on olfactory cues to improve wildlife management outcomes.

Laboratory and field experiments on a range of different taxa have predominantly found that predator odor provokes anti- predator responses, often leading to avoidance by the subordinate species (Apfelbach et al. 2005, Monclús et al. 2005). However, the pervasive assumption that predator odor acts as a deterrent to a subordinate species has been recently questioned. Animals coexist in assemblages of closely related species that often use similar communication systems (Hughes et al. 2010), facilitating the possibility of bidirectional olfactory communication. Stoats and polecats (*Mustela*

putorius) are naturally sympatric in Europe and display commonalities in gland secretions. These species may have evolved communication networks that allow for information exchange (Brinck et al. 1983, Erlinge and Sandell 1988, King and Powell 2007). Encounters between members of the same predator guild are dangerous, as potential gains are unknown and the risks of a confrontation are great (Hutchings and White 2000). Interspecific olfactory communication may diminish these risks by providing information on a competitor without requiring a direct interaction. Recent studies have shown that mesopredators eavesdrop on kairomones; although stoats display subordinate behavior in encounters with larger predators (ferrets *Mustela furo* and cats *Felis catus*; Garvey et al. 2015), the body odor of these dangerous adversaries proved to be a powerful attractant (Garvey et al. 2016). Ferret body odor, which has evolved as a mechanism for communication (Clapperton and Byrom 2005), provoked the strongest attraction, suggesting that coevolution and/ or taxonomic relatedness may magnify responses. Further evidence highlighting the role of odor in mediating predator interactions was provided in a study on foxes (*Vulpes vulpes*), where urine from a dominant (dingo, *Canis dingo*) and a subordinate predator (cat) were investigated with greater frequency than conspecific odor or a control (Banks et al. 2016).

We devised a field experiment to test whether ferret body odor would alter the behavior and detection rates of three of New Zealand's most common invasive mesopredators: stoats (*Mustela erminea*), hedgehogs (*Erinaceus europaeus*), and ship rats (*Rattus rattus*). Hedgehogs and rats are important prey for ferrets, while ferrets dominate stoats in interspecific encounters and are known to kill the smaller mustelid (Wodzicki 1950, Smith et al. 1995). Common prey consumed by these four invasive species include: invertebrates, small mammals, reptiles, amphibians, and the eggs of ground nesting birds (Wodzicki 1950, Murphy and Dowding 1994, Smith et al. 1995, Jones et al. 2005). Additionally, stoats compete with ferrets for lagomorph, rodent, and avian prey (King and Powell 2007). Although these species form novel invasive guilds in New Zealand they are sympatric in parts of their native northern hemisphere range, which is important as evolutionary history is thought to influence the intensity of interactions (Connell 1983).

We examined how ferret odor affected detectability and activity of the three

mesopredator species. We hypothesized that kairomones from a dominant predator would elicit eavesdropping behavior in mesopredators, based on ecological theory and the results of recent studies. We predicted that ferret kairomones would provoke eavesdropping behavior in mesopredators as measured by (1) increased detections at monitoring sites (i.e., site occupancy), (2) increased total number of observations across all monitoring sites, and (3) increased activity (measured as time spent investigating the odor source). We anticipated that mesopredators (4) would approach the ferret odor before approaching a food- based lure at a monitoring site and that (5) ferret odor would remain attractive for longer than a food-b ased lure. In the field experiment, deer (*Cervus* spp.) served as a procedural "control," as detections of this large herbivore should be unaffected by ferret odor. We predicted that deer would (6) show no change in occupancy, number of observations, or activity in response to ferret odor.

Methods

Study location

This study was conducted on Toronui station, a sheep and cattle farm in the Hawke's Bay region of the North Island, New Zealand (39°10′ S, 176°46′ E). The landscape is dominated by pasture, with patches of forest consisting of mixed broadleaf angiosperm species at lower elevations and ma¯nuka (*Leptospermum scoparium*) and ka¯nuka (*Kunzea robusta*) at higher elevations. There was no recent history of predator control at our study area.

The study ran for 64 days, from January to March 2014. Twenty camera monitoring sites were established within and adjacent to forest patches ≥ 50 ha. Average distance between sites was 2.44 km, with a minimum distance of 900 m, to maintain spatial independence and to ensure that olfactory responses at a monitoring site were unlikely to be biased by other sites. Fourteen sites were established at the forest/pasture margin and a further six sites were placed within a forest patch. Forest margins are used extensively by cryptic predator species (Morris and Davidson 2000), so these areas were selected to maximize the likelihood of detection.

Study species

Ferrets are the second largest terrestrial predator in New Zealand, after feral cats, and are the largest of three introduced mustelid species (Wodzicki 1950). Ferrets predominantly use olfaction to communicate, depositing enduring odors that proclaim territorial boundaries or signal reproductive

receptiveness (Clapperton 1989). Chemicals secreted from glands on the chin and neck are deliberately rubbed onto surfaces, often when caching food or after a new den site has been established (Clapperton 1989). Ferrets, as with all mustelids, possess ventral glands (Macdonald 1985) and scent marks have evolved to convey detailed information to conspecifics on the social, reproductive, and health status of the depositing individual (King and Powell 2007, Hughes et al. 2010). Stoats are a highly successful alien predator, designated as one of the world's 100 worst invasive species (Lowe et al. 2000). They occur predominantly in forests, but also in grassland, and are one of the primary agents of decline for over half of all forest birds currently threatened in New Zealand (King and Powell 2007, Innes et al. 2010). Stoat populations can fluctuate due to resource pulses of prey, making them elusive when at low densities in certain environments, seasons, or in particular years (King and Powell 2007). They have keen olfactory senses that are employed to track prey, and for intraspecific communication (Erlinge and Sandell 1988). Our study was conducted in January– March, when the stoat breeding season has completed and sub- adults are actively searching for new territories (King and Powell 2007).

Hedgehogs were introduced primarily to help reduce garden pests, but have become major pests themselves, preying on native insects, reptiles, and the eggs/fledglings of ground-nesting birds. Introduced onto offshore islands in the UK, hedgehog predation resulted in dramatic declines in wading birds (Jackson and Green 2000). Hedgehogs are found across a range of habitats and primarily employ olfaction while foraging for food (Wodzicki 1950, King 2005).

Ship rats arrived as stowaways on ships and have successfully invaded many islands worldwide, including those of New Zealand (Russell and Clout 2005). They are generalist foragers and are associated with extinctions or declines of numerous indigenous species including reptiles, flightless invertebrates, burrowing seabirds, and passerines (Towns et al. 2006).

Ferret odor

Body odor from captive ferrets was collected by placing a clean towel in their bedding area, where it would be in direct contact with the donor animal. Predator body odor has stronger endocrine and behavioral effects on prey than other odors such as urine or feces, as it may indicate a high likelihood that the predator is nearby (Apfelbach et al. 2005). Male ferrets were selected as donor animals as male body odor is more pungent due to

greater concentrations of an aromatic compound (indole), and males are a greater threat to mesopredators by virtue of their size (Clapperton et al. 1988). Towels were placed in the bedding area of individual ferrets for 1 month to ensure the material was thoroughly impregnated with odor. Towels were inspected to remove any excreta before being cut into 15- cm^2 segments and stored in a freezer (−80°C) until required, up to a maximum duration of 2 months**.**

Ferret odor was tested alongside rabbit meat, which is the standard lure used to trap carnivores in New Zealand (Wodzicki 1950, Pierce et al. 2007), to assess whether it could improve the detection rate of mesopredators. A previous pen trial had tested stoats' response to three odor treatments: rabbit meat, ferret odor, and rabbit meat + ferret odor combined (G. Morriss, *unpublished data*). The grouping of both odors together provoked the greatest attraction for stoats and therefore our field trial compared the rabbit + ferret treatment against the rabbit treatment. Comparing various bait types for stoats, Pierce et al. (2007) found that fresh rabbit meat was the most effective. Rabbit meat typically remains in traps for periods ranging from 1 to 3 weeks, but this can be extended to several months where site access is constrained (McMurtrie et al. 2011).

Perforated plastic vials were used to allow odor volatiles to disperse while preventing removal of the lure. Each vial (9 × 3 cm) was drilled with ~50 holes that were 5 mm in diameter. Two vials were used at each monitoring site, one placed at the base of a steel post, with the second placed 20 cm from the base, enabling us to distinguish between approaches to a specific container. Vials were secured to the ground using pegs to ensure that the camera remained trained on the container. The standard size of a vial was used as a reference to estimate the head-body- tail length of *Rattus* spp., which facilitates identification. We randomly deployed one of two possible treatments at each site. For the first treatment one vial received a portion of rabbit meat (3 g), while the second vial remained empty. For the second treatment, rabbit meat was again added to one vial, but the second vial contained 15 cm of towel that had been impregnated with ferret body odor. Each treatment was deployed at one- half of the sites for the first 32 days, and rotated across sites for the second 32- day period, which ensured all sites received each treatment over the study.

Camera trapping

A total of 40 infrared cameras, triggered by heat and/or motion, were deployed for the

study. Cameras were placed in pairs (matched by model type) at each monitoring site, one mounted horizontally and one vertically. Four types of cameras were used: Reconyx Hyperfire PC 900 (26) (Reconyx, Holmen, Wisconsin, USA), LTL Acorn Ltl 5210A (10) (Shenzen LTL Acorn Elegronics, Sanzao Town, Jinwan District, China), Moultrie M990i (2) (Moultrie, New Zealand) and Bushnell (2) (Bushnell Outdoor products, Overland Park, Kansas, USA). Detection efficiency may vary between models (Glen et al. 2013), but cameras were assigned to a monitoring site for the entire study, to ensure consistency across treatments.

The design of our study was influenced by the attributes of our focal species (stoat/hedgehog/rat). In habitat (pasture and native bush) similar to our study area, the average home ranges (male–female) are: stoats, 145–75 ha; hedgehogs, 9.6–4.2 ha; and ship rats, 3.76–1.06 ha (King 2005). These home ranges informed our decision on camera spacing so that we reduced the risk of detecting the same individual at multiple monitoring sites (Rovero and Marshall 2009). Smith et al. (2015) recommended a spacing of <700 m to ensure a control device is encountered by a female stoat. As stoats have the largest home ranges of the targeted mesopredators, we set the spacing of monitoring sites at a minimum of 1 km to minimize multiple recordings of the same individuals, although two sites were 900 m apart due to logistical constraints.

The optimum camera orientation when photographing small mammals depends on the target species, although the most suitable orientation has even been shown to vary between studies on the same species (Smith and Coulson 2012, Taylor et al. 2014). We therefore evaluated two orientations and decided a posteriori on the optimum configuration for our target mesopredators. Vertical cameras were mounted on a steel post, facing downwards from 1.5 m above the ground, with the vials placed in the center of the field of view. Horizontal cameras were mounted on timber stakes 1.5 m away from the base of the steel post. These cameras were mounted 5 cm above ground level, which is approximately the shoulder height of the target mesopredators. All cameras had identical settings or as close as possible where slight variations existed between models: high sensitivity, three photographs per trigger, and no delay between triggers. Vegetation was removed to allow for an unobstructed field of view and to minimize false triggers. Camera batteries and memory cards were replaced after the first month.

Metadata (date, time, location) were extracted from the images using R v. 2.14.1 (R Development Core Team 2015); the function designed for this process, and associated information is provided in supporting material (Data S1: Metadata S1).

Data recording and analysis

Cameras that were orientated horizontally documented the greatest number of species, both in terms of observations (independent record of an individual) and total number of photographs. We therefore chose the horizontal orientation at all sites, with the vertical orientation only selected when the horizontal camera was out of commission. We considered the selected camera at each monitoring site to be an independent sampling unit.

Data were analysed for differences in observations or behavior of the target mesopredators, following the addition of ferret odor. To distinguish photographs of separate animals from repeated photographs of the same individual, we plotted histograms of the time elapsed between consecutive photographs for each species (Brook et al. 2012). Most consecutive photographs of the same species occurred <5 minutes apart, suggesting that these were repeated detections of an individual during one visit to the monitoring site. We considered records of a species to be independent at a monitoring site if detections were separated by more than 30 minutes, unless individuals could be distinguished. The following variables were calculated (1) observation rate, (2) triggers per observation, (3) site occupancy, (4) observations per period, and (5) mesopredator behavior. A summary of the response variables and related predictions are included in Table 1. *Observation rate* was defined as the number of observations per 100 trap days (1 trap day = 1 camera trap set for 24 h; Rovero and Marshall 2009, Glen et al. 2014). Cameras were set to record in bursts of three photographs each time they detected motion; we refer to each burst with at least one image of an animal as a trigger. The *observation rate* of mesopredators is a consequence of an individual's detection of the odor and subsequent behavioral response. These factors will change as a scent attenuates or the perceived value of investigating an odor changes. *Triggers per observation*, an index of a species activity within the camera's field of view, were calculated at each monitoring site: number of camera triggers divided by number of independent observations. A mesopredator's behavioral responses and engagement with an odor will directly influence the time spent

in front of a camera and the variable *triggers per observation* captures this information.

Table 1. Predictions and associated response variables.

Prediction	Response variable
(1) Kairomone (ferret odor) will increase detections at a monitoring sites	(a) independent observation, (b) observation rate, (c) site occupancy
(2) Kairomone will increase total observations across all sites	observation rate, site occupancy
(3) Kairomone will increase activity at a site	(d) triggers per observation, (e) mesopredator behaviors
(4) Kairomone will be initially approached in preference to rabbit odor	mesopredator behaviors
(5) Kairomone will sustain attraction over time	(f) observations per period, triggers per observation
(6) Kairomone will not influence deer behavior	observation rate, site occupancy, triggers per observation

Notes: (a) A species record was defined as an *independent observation* if detections were separated by more than 30 minutes (unless individuals could be distinguished). (b) *Observation rate* was the number of observations per 100 trap days (1 trap day = 1 camera trap set for 24 h). (c) *Site occupancy* is a binary response variable with 1 indicating a species was detected at the monitoring site and 0 indicating non-d etection. (d) *Triggers per observation* is the number of camera triggers divided by number of *independent observations*. (e) *Mesopredator behaviors* were a group of behaviors including cautious approach, scent marking, contact sniffing, self- anointing, and biting of the odor vial. (f) *Observations per period* are independent observations in each period of 8 days.

Site occupancy is a binary response variable with 1 indicating a species was detected at the monitoring site at least once during the study, and 0 indicating non-d etection. Mesopredator *site occupancy* will be determined by a species' abundance and range, but occupancy will also be a function of the detection probability, which may be influenced by the odor treatment. Occupancy models that explicitly account for imperfect detection provide an index of abundance for species without identifiable markings (Meek et al. 2014). *Site occupancy* was used as the binomial presence/absence measure of a

species at a site (MacKenzie 2006). Accurate estimation of species occupancy should account for imperfect detection, i.e., a species may be present at a site but not detected (MacKenzie 2006). This requires sufficient data to estimate detection probability. When detections were too few to estimate detection probability, naïve occupancy estimates were calculated. These ignore detection probabilities and will therefore be biased low. Monitoring periods were divided into intervals of 5 days and we ran a single species single season model framework to estimate occupancy in the software package PRESENCE 9.0 (Hines 2006). We also divided the 32-d ay treatment period into four intervals of 8 days. An 8-day interval is comparable to the weekly re-baiting protocol used for most trapping operations (e.g., McMurtrie et al. 2011) and this enabled us to analyze change over an operational time scale. *Observations per period* are the *independent observations* in each period of 8 days for each species, and cameras active for shorter durations were excluded from the analysis. *Observations per period* will reveal changes in mesopredator behavioral responses over time, as a scent attenuates or the value of investigating the potential resource diminishes.

Mesopredator behaviors were recorded that may help to explain responses to dominant predator odor. These included cautious approach, scent marking, contact sniffing, self- anointing, and biting of a lure vial. We were able to categorize *mesopredator behaviors* from images as they each had distinct, recognizable, body movements. Cautious approach was assessed by the mesopredator's body posture on its initial approach and also by the time taken for the individual to reach the vial after triggering the camera. Contact sniffing was defined as touching a vial with the nose or tongue and we recorded which odor vial was first contacted on a visit. Self-a nointing behavior is defined as an animal spreading its odor through its pelage by licking, which may act as a deterrent to predators (Weldon 2004). We analysed the effect of the ferret odor using generalized linear mixed models (GLMM), from the MASS package in R (Venables and Ripley 2002), which enabled us to assess the influence of fixed and random effects. The response variables for the analysis were *observation rate* and *triggers per observation*. A Poisson error distribution was selected as we had continuous count data (Venables and Ripley 2002). The fixed effect included in the model was "treatment" (rabbit or rabbit + ferret)

and “order” (first or second), while “site” was entered as a random effect, to account for the non-i ndependence of errors associated with repeated measures on the same monitoring site. The fixed effect “order” was included in the model to test whether the deployment of a treatment at a site influenced mesopredator detections in the following period. Models were assessed by plotting the residuals and testing for overdispersion. Where results of the GLMM revealed significant treatment effects, we constructed additional species models for the four 8-d ay time periods, with the response variables *observations per period* and *triggers per observation*, to assess each period’s contribution to the significant result. Differences in mesopredator *site occupancy* and additional *mesopredator behaviors* were assessed using Fisher’s exact test. To reduce the risk of experiencing a Type 1 error as a result of conducting multiple comparisons, we used the Benjamini- Hochberg method to control for the false discovery rate (FDR; Benjamini and Hochberg 1995). This approach provides greater power than conventional Bonferroni- based methods, balancing the risk between Type I and Type II errors by describing the proportion of significant tests that are actually null (Verhoeven et al. 2005, Waite and Campbell 2006). We interpret $P \leq 0.05$ as significant if the FDR equivalent of a P value was also ≤ 0.05. All statistical analyses were performed in the R environment (version 2.14.1, R Development Core Team 2015).

Table 2. Summary of sampling effort and camera trapping results for the response of mesopredators (stoat, hedgehog, and ship rat) to the body odor of a dominant predator (ferret).

Species	Cameras set (functioning)	Camera days (mean)	Cameras with at least one detection	Total no. triggers	Total no. observations	Observation rate
Rabbit		566				1.41
treatment		(29.78)				16.78
Stoat		566				13.07
Hedgehog		(29.78)				4.59
Rat	20 (19)	566	4	26	7	
Deer	20 (19)	(29.78)	17	318	95	
	20 (19)	566	13	258	74	
	20 (19)	(29.78)	6	86	26	
Rabbit +		524				
ferret		(27.57)				
treatment		524				
Stoat	20 (19)	(27.57)	11	155	28	5.34
Hedgehog	20 (19)	524	16	856	162	30.92
Rat	20 (19)	(27.57)	13	281	98	18.70
Deer	20 (19)	524	7	97	28	5.34
		(27.57)				

Note: The definitions of *trigger, observation*, and *observation rate* are given in Table 1.

results

Camera trapping effort

Sampling effort totalled 1834 trap days for the 20 paired cameras, when both orientations were included. Two monitoring sites were removed from the analysis, one due to cattle disturbance and a second due to flooding. With the horizontal camera preferentially selected, there were 1090 trap days for analysis.

Observation rate and observations per period

Collectively across all sites, there were 465 independent observations of the three mesopredators: 288 with the ferret odor and

177 without, a 63% overall increase with the addition of the kairomone (Table 2). There was a corresponding increase in the overall *observation rate* for all three mesopredators. Also the number of mesopredator *observations per period* was greater with the addition of the ferret odor, and these differences were significant in periods 3 and 4 (Fig. 1).

Hedgehogs (55%) were the most frequently detected species based on *observation rate*, followed by rats (37%) and stoats (8%). The order of the treatments did not

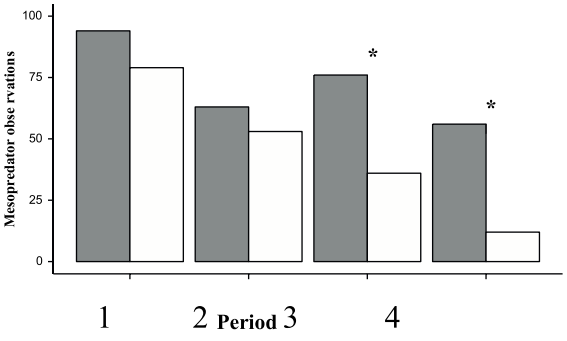


Fig. 1. Mesopredator (stoat/hedgehog/rat) *observations per period* for each of the four 8- day time periods. Treatments are represented by grey bar (rabbit + ferret) and white bar (rabbit). Asterisks denote a significant difference between treatments at ($P < 0.05$). [Color figure can be viewed at wileyonlinelibrary.com]

influence mesopredator *observation rate* (GLMM; $P = 0.74$). There was a significant increase in stoat *observation rate* with the addition of ferret odor (Fig. 2, Table 3). Stoats made up 10% of observations with rabbit + ferret odor and 5% with rabbit only. In addition to stoats, one ferret was detected at the rabbit treatment and a ferret and weasel (*Mustela nivalis*) were detected at the kairomone treatment. Treatment type did not significantly influence the number of observations or the *observation rates* for rats or deer (Fig. 2, Table 2) and there was some evidence of increased *observation rate* for hedgehogs. Stoat *observations per period* were higher at sites with ferret odor than those without, and there was a particularly marked difference after the first period (Table 4). Increases were also recorded for the hedgehog *observation rate*, with the deviation most pronounced in the third and fourth period (Table 4).

Triggers per observation

There were 6861 photographs taken of the target mesopredators, 4744 with the ferret and rabbit combination and 2117 with rabbit only, an overall increase of 124% with the addition of the ferret odor. The most photographed mesopredators were hedgehogs (71%), followed by rats (22%), and then stoats (7%). Treatment order did not influence *triggers per observation* for

mesopredators (GLMM; $P = 0.37$). For hedgehogs, *triggers per observation* were significantly higher with the addition of the ferret odor, particularly in the first and second period (Table 4, Fig. 3). There was some evidence that *triggers per observation* for stoats were different for the entire month and significant differences were recorded in three of the four monitoring periods (Table 4, Fig. 3). Rats had fewer *triggers per observation* with the addition of ferret odor in period 1, but there were no differences in subsequent periods (Fig. 3).

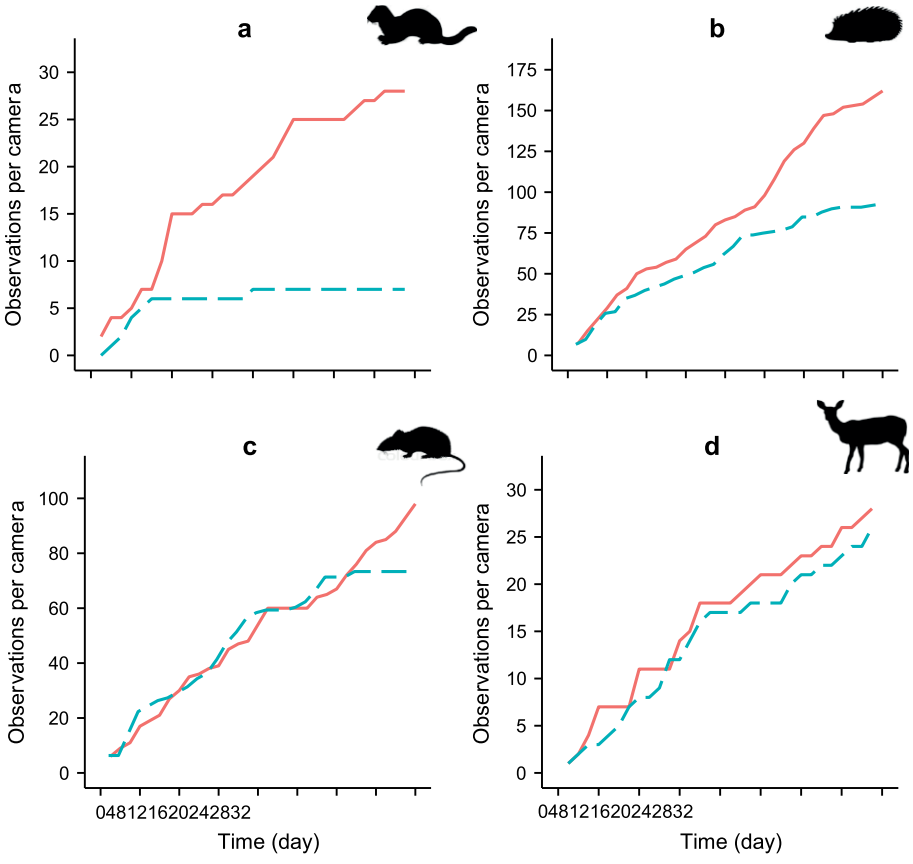


Fig. 2. Cumulative observations per active camera, recorded over the 32- day treatment period for (a) stoat, (b) hedgehog, (c) rat, and (d) deer. Treatments are represented by solid red line (rabbit + ferret) and dashed blue line (rabbit). [Color figure can be viewed at wileyonlinelibrary.com]

Site occupancy

Fisher's exact test showed a significant increase ($P = 0.04$) in the number of sites where stoats were detected using rabbit + ferret odor, as compared to rabbit only. There was no difference in the number of sites with detections of hedgehogs ($P = 0.65$), rats ($P = 0.95$), or deer ($P = 0.93$). Stoats were detected at only 4 of 19 sites (21%) with the

rabbit treatment, but were recorded at 11 of 19 sites (58%) with the addition of the ferret kairomone (Fig. 4; Appendix S1: Fig. S1). Average distances between pairs of cameras that detected stoats were 1.5 km (maximum = 2.1 km, minimum = 0.9 km). Estimates of occupancy and distribution for rats and hedgehogs were similar with both treatments (Appendix S1: Fig. S1).

Mesopredator behaviors

In instances where the treatment employed was ferret odor and rabbit, we recorded 20 occasions where a stoat made contact with a lure vial on its first approach. The vial containing ferret odor was contacted on 15 of these

Table 3. General linear mixed models (GLMM) results for responses by mesopredators to ferret odor based on *observation rate* and *triggers per observation*.

Source of variation	Value	SE	df	*t*	*P*
Observation rate (model: GLMM, Poisson distribution) Stoat	1.46	0.27	18	5.34	**<0.0001†**
Hedgehog	0.57	0.21	18	2.7	0.0158
Rat	0.22	0.2	18	0.83	0.29
Deer	0.15	0.35	18	0.44	0.66
Triggers per observation (model: GLMM, Poisson distribution) Stoat	1.1	0.49	18	2.23	0.0397
Hedgehog	0.81	0.28	18	2.94	**0.0091****
Rat	0.32	0.26	18	0.51	0.62
Deer	0.37	0.24	18	1.53	0.14

Notes: GLMM tested for difference between treatments: rabbit vs. rabbit + ferret odor. *P* values are in boldface type if they remained significant (≤0.05) after controlling for a false-discovery rate (FDR) of 5%. ***P* < 0.01; †*P* < 0.0001.

Source of variation	Value	SE	df	*t*	*P*
Total mesopredator observation	0.17 0.2	0.2	17	0.85	0.41
rate (Poisson) Period 1	0.82	0.32	16	0.65	0.52
Period 2	1.67	0.23	15	3.61	**0.0025****

Period 3		0.41	8	4.06	**0.0036****
Period 4					
Stoat observation per period					0.06
(Poisson)					**<0.0001†**
Period 1	0.61	0.49	17	2.05	**0.0348**
Period 2	20.07	0.28	16	411.98	**<0.0001†**
Period 3	1.86	0.8	15	2.32	
Period 4	26.07	0.151	8	171.52	
Hedgehog observation per period					0.5
(Poisson) Period 1	0.18	0.26	17	0.68	0.26
Period 2	0.33	0.28	16	1.17	**0.015**
Period 3	0.95	0.34	15	2.74	0.056
Period 4	1.1	0.048	8	2.22	
Stoat triggers per observation					**0.027**
(Poisson)					**<0.0001†**
Period 1	0.88	0.48	17	2.42	**0.026**
Period 2	21.24	0.37	16	450.38	**<0.0001†**
Period 3	2.19	0.41	15	2.48	
Period 4	27.49	0.98	8	3475	
Hedgehog triggers per observation					
(Poisson) Period 1		0.34	17	2.74	**0.015**
Period 2	0.94 2	0.43	16	4.66	**0.0003*****
Period 3	0.47	0.34	15	1.38	0.18
Period 4	0.43	0.43	8	1	0.34

Table 4. GLMM results for *observation rate, observations per period,* and *triggers per observation* for stoats and hedgehogs in each period.

Notes: These two species displayed evidence of a treatment effects (Table 3). GLMM tested for difference between treatments: rabbit vs. rabbit + ferret odor. *P* values are in boldface type if they remained significant (≤0.05) after controlling for a false- discovery

rate (FDR) of 5%. $^{**}P < 0.01$, $^{***}P < 0.001$, and $\dagger P < 0.0001$.

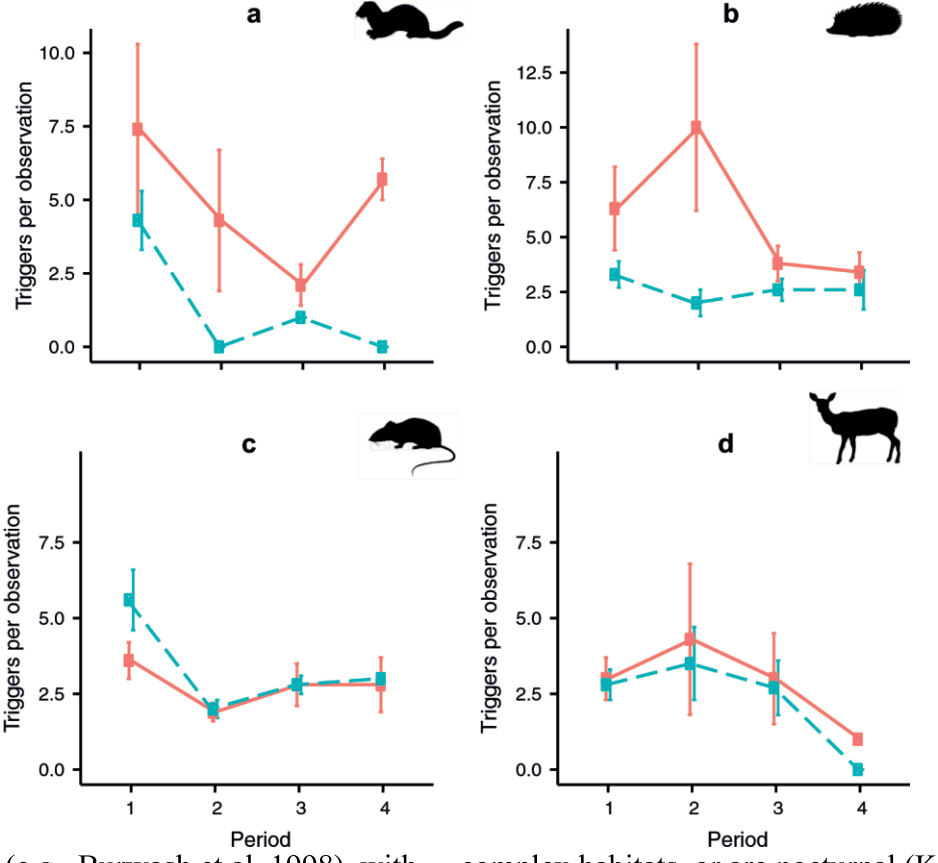
occasions, whereas the rabbit meat lure was contacted on 5 occasions. There were 5 instances where stoats cautiously approached the ferret odor vial, yet similar slow deliberate movements were never recorded when rabbit meat was the sole lure. Scent marking by stoats, when the treatment included ferret odor, was observed on 6 occasions, once by body rubbing with the head/neck and otherwise by anal drag (Appendix S1: Fig. S2). Scent marking by stoats was not recorded when rabbit meat was the treatment and no scent marking was recorded by other mesopredators.

Hedgehogs engaged with the ferret lure for greater durations than any other mesopredator, repeatedly circling the vial. Self- anointing was recorded on 33 occasions at monitoring sites with ferret odor, but never with the rabbit meat treatment. This behavior appears not to be age specific, as it was recorded for hedgehogs of all sizes (Appendix S1: Fig. S3).

Rats attempted to bite into the kairomone vial on nine occasions, with most instances occurring (7/9) in the latter half of the trial; this behavior was only recorded for vials with ferret odor (Appendix S1: Fig. S4).

Discussion

Our results support the prediction that kairomones from an apex predator should provoke eavesdropping by mesopredators, significantly increasing detections for stoats. Ferret body odor remained attractive for the duration of the experiment whereas detections with rabbit meat decline steadily with time. Apex predator kairomone was engaged by hedgehogs for shorter durations as its freshness diminished, while stoats continued to maintain their interest in the latter stages of the trial. Inspection of aged predator cues is a relatively low-c ost activity, but the quality of information available in a scent recedes as the freshness declines (Bytheway et al. 2013). The most marked responses to ferret odor were discerned for stoats. Stoat observations increased four- fold, their estimated *site occupancy* changed from rare to widespread, and stoats engaged with the rabbit + ferret treatment for substantially longer than the rabbit treatment. Hedgehogs also approached lures containing ferret odor more frequently and for s ignificantly longer periods than lures with rabbit meat. Rat observation rates at the end of the first period were slightly greater with the addition of the kairomone, yet *triggers per observation* for a detected individual were 50% lower. Other studies have demonstrated rat avoida nce of fresh



kairomones (e.g., Burwash et al. 1998), with these responses diminishing as the predator cue aged (e.g., Apfelbach et al. 2005, Bytheway et al. 2013). Over the entire length of the trial, our results suggest that wild rats were not significantly attracted or repelled by ferret odor. These results concur with studies that have demonstrated no evidence that predator odor reduced (e.g., Bramley and Waas 2001) or increased (Banks 1998) rat detections over longer durations.

FiG. 3. *Triggers per observation* (mean ± SE) for the four time periods for (a) stoat, (b) hedgehog, (c) rat, and (d) deer. Treatments are represented by solid red line (rabbit + ferret) and dashed blue line (rabbit). [Color figure can be viewed at wileyonlinelibrary.com]

Chemical cues make an uncertain world more predictable and olfaction is particularly important for species that are solitary, inhabit complex habitats, or are nocturnal (Kats and Dill 1998). When prey encounter predator scent, avoidance may be the optimum defense, and prey frequently avoid a detected kairomone (e.g., Dickman and Doncaster 1984, Je˛drzejewski et al. 1993). However, mesopredators, particularly highly mobile species, encounter a myriad of chemical cues that potentially provide a rich source of information (Bytheway et al. 2013). Careful evaluation of a kairomone is needed to determine the direction in which a predator travelled, which can be assessed by variation in odor intensity along a scent trail. Informed prey are more difficult to capture and as

stoats and hedgehogs are predominantly solitary foragers, these species should gain greater benefit from eavesdropping than gregarious species that can be warned by conspecifics (Ridley et al. 2014). However, inspection behavior is not without risk as the scent depositing predator may remain in the vicinity or an intended recipient (conspecifics) could be attracted to the odor. The persistence of eavesdropping behavior suggests that kairomone investigation provides fitness benefits to a species, despite the associated danger.

Close approach to the predator odor may be necessary to activate the appropriate olfactory receptors. The vomeronasal organ (VNO), which is a chemoreceptor, detects non- volatile compounds and requires direct physical contact with the source (Papes et al. 2010). Most mammals, including studied Mustelidae such as ferrets, possess a functioning vomeronasal organ (Estes 1972, Woodley et al. 2004). The purpose of the VNO was thought to primarily relate to the detection of chemical cues from conspecifics, but recent discoveries have demonstrated that, when the VNO is destroyed, it inhibits an animal's ability to perceive predator odor (Zhao and Liu 2015). Mesopredators may therefore approach the predator scent to assess non- volatile compounds encoded in the chemosignal. This need for direct contact suggests that predator odor could be an effective attractant, as it increases the likelihood of a target species interacting with a camera trap or control device.

The response of stoats to ferret odor differed from those of other mesopredators. This may be because stoats are primarily competitors

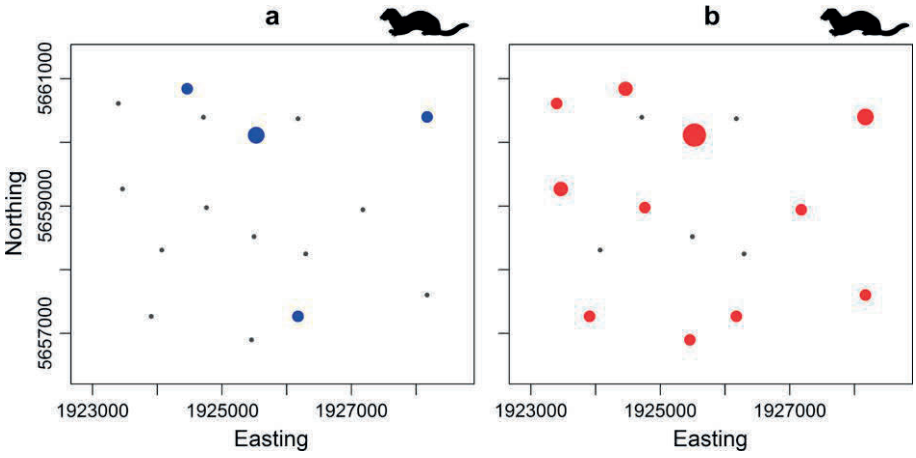


Fig 4. Stoat site detections with (a) rabbit (blue points) or (b) ferret + rabbit (red points). The size of a point indicates the number of observations at a particular monitoring site. Monitoring sites that did not detect stoats are illustrated with black dots. Distance between consecutive tics on the *x* and *y* axis are 1 km. [Color figure can be viewed at wileyonlinelibrary.com]

of ferrets, whereas the other mesopredators are primarily prey. A kairomone may provide important additional information to a competitor, such as the foraging activity of a rival species (van Dijk et al. 2008) or the location of common den sites (Dowding and Elliott 2003), whereas the freshness of the scent may be the most important characteristic for prey, facilitating risk assessment (Bytheway et al. 2013). Stoats, given their greater agility, would be at less risk of injury or death than the other mesopredators if a ferret was encountered in an open area. Mesopredator' responses may therefore be additionally influenced by the level of risk posed by the dominant predator. Increased stoat detections across sites with the addition of the kairomone are more likely the result of multiple stoat detections, rather than increased activity by a few stoats. The average home range of a stoat (King and Powell 2007) equates to a diameter of 1.36 km (male) and 0.98 km (female), based on a circular home range. Using these estimates and stoat detections across sites, there was one pair of cameras that a female could travel between and three pairs that a male could travel between, at the maximum extent of an average home range. Home ranges of stoats overlap within and between the sexes in all seasons (King and Powell 2007). Breeding

cycles would not influence stoat detections, but dispersing sub- adults could appear or reside in our study area. Given the topography of the study area, distances between cameras, and overlapping home ranges, it is more likely that we detected multiple stoats. Similarly, detections of other mesopredators are unlikely to be a function of movement given the distances between cameras and the circular diameter of home ranges: rat (male 0.22 km and female 0.11 km) and hedgehog (male 0.35 km and female 0.23 km).

Visits by mesopredators may have increased the olfactory information available at a monitoring site. Kairomones have been shown to influence the behavior of sympatric predators (Garvey et al. 2016) and the build-up of chemical information at a site may influence subsequent visitations. Odors deposited unintentionally, as an individual moves around in its environment, would attenuate quickly and their attractiveness would be superseded by fresher odor deposits. However, odor signals (scat, urine, or body odor) that are deposited intentionally, may persist for longer in the environment and these signals may create a web of information among sympatric predators (Banks et al. 2016). Stoats were the only mesopredator recorded intentionally scent marking beside the ferret odor, both by body rubbing and defecating, which occurred during 21% of observations. This behavior is difficult to explain if the subordinate species wished to remain inconspicuous. Based on our information, scent marking did not increase the detection probability of conspecifics or sympatric mesopredators, as visitation rates were consistent before and after scent marking. However, there were only six documented instances of scent marking, which makes these results inconclusive.

Mesopredators may be attracted to dominant predator odor to locate prey, carrion, or den sites, as eavesdropping for resources occurs between species that occupy the same trophic levels (Peake 2005, van Dijk et al. 2008). Stoats do not make their own dens, but use those of other animals (King 2005) and may eavesdrop on ferret scent to help locate appropriate sites. In support of the idea that stoats investigated the odor to acquire resources, one study that radio-t racked mustelids recorded nine occasions where dens were shared sequentially by both ferrets and stoats (Dowding and Elliott 2003). Scavenging for food may also potentially explain attraction to kairomones, as stoats, hedgehogs and rats may associate aging

ferret odor with the possibility of locating the partial remains of prey.

Our study fell within the breeding season of hedgehogs in New Zealand (King 2005) and the attraction displayed by hedgehogs, i.e., repeatedly circling the kairomone vial, is a behavior that appears very similar to the "cartwheeling" performed by males during courtship (King 2005). Hedgehogs were also photographed self- anointing on more than 30 occasions: they are known to self-a noint with a range of novel, strong- smelling, or toxic substances.

The basis of this behavior is unknown; it may act as a deterrent to predators or alternatively self-a nointing may play a role in mating behavior (Weldon 2004, King 2005).

Management applications

A major challenge for controlling invasive species is monitoring populations at low densities. Responses to a dominant predator odor, such as increased attraction and engagement, can be exploited to improve conservation outcomes and the reliability of monitoring information. Exotic species that decline after intervention, or invade new ecosystems, are acutely aware of established competitors and conspecifics (Pyšek and Richardson 2010). New Zealand's pest- free islands are important refuges for native animals and a kairomone lure could be deployed for long term monitoring and interception. For example, a stoat that invaded Kapiti Island, 5 km off the coast of New Zealand, proved extremely difficult to locate and expensive to remove (Prada et al. 2014). Eventually, after an extensive operation, the stoat and its offspring were captured, with the sole male offspring entering a trap that was treated with the pheromones of a female stoat. Reduction in intraand interspecific competition in managed ecosystems leads to greater resource availability and a non-f ood- based attractant would be advantageous in these situations (Glen et al. 2013). Stoats are extremely difficult to detect at low densities (Choquenot et al. 2001) and monitoring in this study using only a rabbit lure would have substantially underestimated their prevalence. When eradicating an invasive population, it is essential to put all animals at risk and variability in temperament between members of a population leads to inconsistent responses to chemical signals (Réale et al. 2007). Costs of eliminating the last few survivors may be disproportionally high (Nugent et al. 2007) so increasing the range of lures may improve capture rates, thereby ameliorating the costs of mop- up operations. In addition to the management of invasive species, animals are also live-t

rapped for translocation, to collect biological samples, and to fit monitoring devices. The scent of a dominant competitor may always be worth investigating, so a kairomone lure could function effectively in these situations. Our findings could also have applications for invasive mustelid management outside of New Zealand. American mink (*Neovison vison*) are listed as one of 37 invasive alien species by the European Union and member states are required to take measures to ensure early detection and rapid eradication of listed species. Harrington et al. (2009) demonstrated that American mink are attracted to polecat odor. As ferrets are a sub-s pecies of polecats, and considering the results from our study, ferret kairomone may be an effective management tool for mink. Camera traps are being used increasingly in wildlife monitoring, and can operate for extensive periods (Meek et al. 2014). However, most scent lures do not remain attractive for comparable durations. This incongruence between camera capabilities and lure viability may lead to inefficient monitoring devices or require labor-intensive refreshing of lures. Ferret pheromones have evolved to endure in the environment to maximize the probability of interception (Clapperton 1989), making pheromones an ideal natural long- life lure. Camera traps can also help assess wildlife populations by identifying naturally marked animals, a powerful nonintrusive technique requiring clear images to distinguish among individuals (Trolle and Kéry 2003). Increasing an animal's engagement at a monitoring site would help to reduce the number of unidentified individuals. Similarly, hair collected for DNA analysis requires the target species to interact with sampling devices. The significant increase in engagement observed by two mesopredators in our study suggests that dominant predator odor could be exploited in these situations. Olfaction is the main sensory perception in many mustelids yet its potential role in wildlife management has not yet been fully realized. Monitoring with ferret kairomones changed our assessment of stoat abundance and distribution. Mustelidae are often considered rare, due to limited reliable records, making it difficult to accurately assess their distribution, abundances, and therefore their appropriate conservation status (Ramírez-C haves et al. 2016). For example, accurate assessment of populations of cryptic mustelids, such as the marbled polecat (*Vormela peregusna*), Patagonian weasel (*Lyncodon patagonicus*), and Colombian weasel (*Mustela felipei*) are hampered by very low sighting rates and a

scarcity of records (Ramírez- Chaves et al. 2016). The use of ferret kairomones to aid in the monitoring of these species may therefore generate more reliable population estimates. The technique of using dominant predator body odor could also potentially assist in reducing native mesopredator naivety to invasive predators or increasing the success of reintroduction programs for endangered native species. The critically endangered black footed ferret (*Mustela nigripes*) experiences 80% reintroduction mortality due to interference competition (Biggins et al. 2011). Ferret odor could potentially be deployed to encourage activity in particular areas of the habitat, to help with population monitoring, and dominant predator body odor could be used for pre- release behavior conditioning (Kleiman 1989, Biggins et al. 2011, Smith and Blumstein 2012). Studying olfactory communication provides insights into predator ecology, but it is also of applied importance for population monitoring and invasive species management. Deploying dominant predator kairomones to monitor other predators may be a technique that is applicable worldwide. We hope our findings have practical applications for wildlife management and that future research continues to investigate the role of chemical communication among competing predators.

literature cited

Apfelbach, R., C. D. Blanchard, R. J. Blanchard, R. A. Hayes, and I. S. McGregor. 2005. The effects of predator odors in mammalian prey species: a review of field and laboratory s tudies. Neuroscience and Biobehavioral Reviews 29:1123–1144.

Banks, P. B. 1998. Responses of Australian bush rats, *Rattus fuscipes*, to the odor of introduced *Vulpes vulpes*. Journal of Mammalogy 79:1260–1264.

Banks, P. B., A. Daly, and J. P. Bytheway. 2016. Predator odours attract other predators, creating an olfactory web of information. Biology Letters 12:361–363.

Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society Series B (Methodological) 57:289–300.

Biggins, D. E., B. J. Miller, L. R. Hanebury, and R. A. Powell. 2011. Mortality of Siberian polecats and black-f ooted ferrets released onto prairie dog colonies. Journal of Mammalogy 92:721–731.

Bramley, G. N., and J. R. Waas. 2001. Laboratory and field evaluation of predator odors as repellents for kiore (*Rattus exulans*)

and ship rats (*R. rattus*). Journal of Chemical Ecology 27:1029–1047.

Brinck, C., S. Erlinge, and M. Sandell. 1983. Anal sac secretion in mustelids: a comparison. Journal of Chemical Ecology 9:727–745.

Brook, L. A., C. N. Johnson, and E. G. Ritchie. 2012. Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. Journal of Applied Ecology 49:1278–1286.

Burwash, M. D., M. E. Tobin, A. D. Woolhouse, and T. P. Sullivan. 1998. Laboratory evaluation of predator odors for eliciting an avoidance response in roof rats (*Rattus rattus*). Journal of Chemical Ecology 24:49–66.

Bytheway, J. P., A. J. R. Carthey, and P. B. Banks. 2013. Risk vs. reward: How predators and prey respond to aging olfactory cues. Behavioral Ecology and Sociobiology 67: 715–725.

Campbell-Palmer, R., and F. Rosell. 2011. The importance of chemical communication studies to mammalian conservation biology: a review. Biological Conservation 144:1919–1930.

Choquenot, D., W. A. Ruscoe, and E. Murphy. 2001. Colonisation of new areas by stoats: time to establishment and requirements for detection. New Zealand Journal of Ecology 25:83–88.

Clapperton, B. K. 1989. Scent-m arking behaviour of the ferret, *Mustela furo*. Animal Behaviour 38:436–446.

Clapperton, B., and A. Byrom. 2005. Feral ferret. Pages 294– 307 *in* C. M. King, editor. The handbook of New Zealand mammals. Oxford University Press, Melbourne, Australia.

Clapperton, B. K., E. O. Minot, and D. R. Crump. 1988. An olfactory recognition system in the ferret *Mustela furo* L. (Carnivora: Mustelidae). Animal Behaviour 36:541–553.

Clout, M. 2001. Where protection is not enough: active conservation in New Zealand. Trends in Ecology and Evolution 16:415–416.

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. American Naturalist 122:661–696.

Dickman, C., and C. Doncaster. 1984. Responses of small mammals to red fox (*Vulpes vulpes*) odour. Journal of Zoology 204:521–531.

Dowding, J., and M. Elliott. 2003. Ecology of stoats in a South island braided river

valley. Department of Conservation, Wellington, New Zealand.
Erlinge, S., and M. Sandell. 1988. Coexistence of stoat, *Mustela erminea*, and weasel, *M. nivalis*: social dominance, scent communication, and reciprocal distribution. Oikos 53:242–246.
Estes, R. D. 1972. The role of the vomeronasal organ in mammalian reproduction. Mammalia 36:315–341.
Ferrari, M. C. O., and D. P. Chivers. 2009. The ghost of predation future: threat-sensitive and temporal assessment of risk by embryonic woodfrogs. Behavioral Ecology and Sociobiology 64:549–555.
Garvey, P. M., A. S. Glen, and R. P. Pech. 2015. Foraging Ermine Avoid Risk: behavioural responses of a mesopredator to its interspecific competitors in a mammalian guild. Biological Invasions 17:1771–1783.
Garvey, P. M., A. S. Glen, and R. P. Pech. 2016. Dominant predator odour triggers caution and eavesdropping behaviour in a mammalian mesopredator. Behavioral Ecology and Sociobiology 70:481–492.
Glen, A. S., S. Cockburn, M. Nichols, J. Ekanayake, and B. Warburton. 2013. Optimising camera traps for monitoring small mammals. PLoS ONE 8:16–24.
Glen, A., B. Warburton, J. Cruz, and M. Coleman. 2014. Comparison of camera traps and kill traps for detecting mammalian predators: a field trial. New Zealand Journal of Zoology 41:155–160.
Harrington, L. A., A. L. Harrington, and D. W. Macdonald. 2009. The smell of new competitors: the response of American mink, *Mustela vison*, to the odours of otter, *Lutra lutra* and polecat, *M. putorius*. Ethology 115:421–428.
Hemmi, J. M., and A. Pfeil. 2010. A multi-stage anti- predator response increases information on predation risk. Journal of Experimental Biology 213:1484–1489.
Hines, J. E. 2006. Program PRESENCE. See https://www. mbr-pwrc.usgs.gov/software/presence.html
Hughes, N. K., E. Korpimäki, and P. B. Banks. 2010. The predation risks of interspecific eavesdropping: weasel-v ole interactions. Oikos 119:1210–1216.
Hutchings, M. R., and P. C. L. White. 2000. Mustelid scent- marking in managed ecosystems: implications for population management. Mammal Review 30:157–169.
Innes, J., D. Kelly, J. M. Overton, and C. Gillies. 2010. Predation and other factors currently limiting New Zealand forest birds. New Zealand Journal of Ecology 34:86–114.
Jackson, D., and R. Green. 2000. The importance of the introduced hedgehog (*Erinaceus europaeus*) as a predator of the

eggs of waders (*Charadrii*) on Machair in South Uist, Scotland. Biological Conservation 93:333–348.

Je˛drzejewski, W., L. Rychlik, and B. Je˛drzejewska. 1993. Responses of bank voles to odours of seven species of predators: experimental data and their relevance to natural predator- vole relationships. Oikos 68:251–257.

Jones, C., K. Moss, and M. Sanders. 2005. Diet of hedgehogs (*Erinaceus europaeus*) in the upper Waitaki Basin, New Zealand: implications for conservation. New Zealand Journal of Ecology 29:29–35.

Kats, L. B., and L. M. Dill. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. Ecoscience 5:361–394.

King, C. M. 2005. The handbook of New Zealand mammals. Oxford University Press, Auckland, New Zealand.

King, C. M., and R. A. Powell. 2007. The natural history of weasels and stoats: ecology, behaviour and management. Second edition. Oxford University Press, New York, New York, USA.

Kleiman, D. G. 1989. Reintroduction of captive mammals for conservation. BioScience 39:152–161.

Long, R. A., P. MacKay, J. Ray, and W. Zielinski. 2012. Noninvasive survey methods for carnivores. Island Press, Washington, D.C., USA.

Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2000. 100 of the world's worst invasive alien species: a selection from the global invasive species database. Invasive Species Specialist Group, Auckland, New Zealand.

Macdonald, D. W. 1985. The carnivores: order Carnivora. Pages 619–722 *in* R. E. Brown and D. W. Macdonald, editors. Social odours in mammals. Clarendon Press, Oxford,
UK.

MacKenzie, D. I. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, Sydney, Australia.

McKinney, M. L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. Annual Review of Ecology and Systematics 28:495–516.

McMurtrie, P., K. Edge, D. Crouchley, D. Gleeson, M. Willans, and A. Veale. 2011. Eradication of stoats (*Mustela erminea*) from Secretary Island, New Zealand. Pages 455–460 *in* C. Veitch, M. N. Clout, and D. R. Towns, editors. Island invasives: eradication and management. IUCN, Gland, Switzerland.

Meek, P. D., et al. 2014. Recommended guiding principles for reporting on camera trapping research. Biodiversity and Conservation 23:2321–2343.
Monclús, R., H. G. Rödel, D. Von Holst, and J. De Miguel. 2005. Behavioural and physiological responses of naive European rabbits to predator odour. Animal Behaviour 70: 753–761.
Morris, D. W., and D. L. Davidson. 2000. Optimally foraging mice match patch use with habitat differences in fitness. Ecology 81:2061–2066.
Murphy, E. C., and J. E. Dowding. 1994. Range and diet of stoats (*Mustela erminea*) in a New Zealand beech forest. New Zealand Journal of Ecology 18:11–18.
Nugent, G., D. R. Morgan, P. Sweetapple, and B. Warburton. 2007. Developing strategy and tools for the local elimination of multiple pest species. Pages 410–417 *in* Managing Vertebrate Invasive Species Conference. National Wildlife Research Centre, Fort Collins, Colorado, USA.
Papes, F., D. W. Logan, and L. Stowers. 2010. The vomeronasal organ mediates interspecies defensive behaviors through detection of protein pheromone homologs. Cell 141:692–703.
Peake, T. M. 2005. Eavesdropping in communication networks. Pages 13–37 *in* P. K. McGregor, editor. Animal communication networks. Cambridge University Press, Cambridge, UK.
Pierce, R. J., N. Miller, E. Neill, C. Gardiner, and M. Kimberley. 2007. Field trials of fresh and long-life stoat baits in Northland, New Zealand. Department of Conservation, Science and Technical Publication, Wellington, New Zealand.
Prada, D., A. Veale, J. Duckworth, E. Murphy, S. Treadgold, R. Howitt, S. Hunter, and D. Gleeson. 2014. Unwelcome visitors: employing forensic methodologies to inform the stoat (*Mustela erminea*) incursion response plan on Kapiti Island. New Zealand Journal of Zoology 41:1–9.
Pyšek, P., and D. M. Richardson. 2010. Invasive species, environmental change and management, and health. Annual Review of Environment and Resources 35:25–55.
R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org Ramírez-Chaves, H. E., J. F. González-Maya, and J. Schipper. 2016. Small Carnivore Conservation and its contribution to the knowledge of rare small carnivores. Small Carnivore Conservation 54:1–3.

Réale, D., S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemanse. 2007. Integrating animal temperament within ecology and evolution. Biological Reviews 82:291–318.

Ridley, A. R., E. M. Wiley, and A. M. Thompson. 2014. The ecological benefits of interceptive eavesdropping. Functional Ecology 28:197–205.

Ritchie, E. G., and C. N. Johnson. 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters 12:982–998.

Roberts, S. C., and L. M. Gosling. 2001. Economic consequences of advertising scent mark location on territories.
Pages 11–17 *in* A. Marchlewska-Koj, J. J. Lepri, and D. Miiller-Schwarze, editors. Chemical signals in vertebrates. Springer, New York, New York, USA.

Rovero, F., and A. R. Marshall. 2009. Camera trapping photographic rate as an index of density in forest ungulates. Journal of Applied Ecology 46:1011–1017.

Roy, S. S., I. Macleod, and N. P. Moore. 2006. The use of scent glands to improve the efficiency of mink (*Mustela vison*) captures in the Outer Hebrides. New Zealand Journal of Zoology 33:267–271.

Russell, J., and M. Clout. 2005. Rodent incursions on New Zealand islands. Pages 324–330 *in* J. Parkes, M. Statham, and G. Edwards, editors. Proceedings of the 13th Australasian Vertebrate Pest Conference. Landcare Research, Lincoln, New Zealand.

Schoeppner, N. M., and R. A. Relyea. 2009. Interpreting the smells of predation: How alarm cues and kairomones induce different prey defences. Functional Ecology 23:1114–1121.

Smith, B. R., and D. T. Blumstein. 2012. Structural consistency of behavioural syndromes: Does predator training lead to multi-c ontextual behavioural change? Behaviour 149: 187–213.

Smith, J. K., and G. Coulson. 2012. A comparison of vertical and horizontal camera trap orientations for detection of potoroos and bandicoots. Australian Mammalogy 34: 196–200.

Smith, G., J. Ragg, H. Moller, and K. Waldrup. 1995. Diet of feral ferrets (*Mustela furo*) from pastoral habitats in Otago and Southland, New Zealand. New Zealand Journal of Zoology 22:363–369.

Smith, D. H., R. Clayton, D. Anderson, and B. Warburton. 2015. Using home-range data to optimise the control of invasive animals. New Zealand Journal of Zoology 39:286–290.

Taylor, B. D., R. L. Goldingay, and J. M. Lindsay. 2014. Horizontal or vertical?

Camera trap orientations and recording modes for detecting potoroos, bandicoots and pademelons. Australian Mammalogy 36:60.
Terborgh, J. 1974. Preservation of natural diversity: the problem of extinction prone species. BioScience 24:715–722.
Towns, D. R., I. A. Atkinson, and C. H. Daugherty. 2006. Have the harmful effects of introduced rats on islands been exaggerated? Biological Invasions 8:863–891.
Trolle, M., and M. Kéry. 2003. Estimation of ocelot density in the Pantanal using capture-recapture analysis of camera- trapping data. Journal of Mammalogy 84:607–614.
van Dijk, J., T. Andersen, R. May, R. Andersen, R. Andersen, and A. Landa. 2008. Foraging strategies of wolverines within a predator guild. Canadian Journal of Zoology 86:966–975.
Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Springer, New York, New York, USA.
Verhoeven, K. J., K. L. Simonsen, and L. M. McIntyre. 2005. Implementing false discovery rate control: increasing your power. Oikos 108:643–647.
Waite, T. A., and L. G. Campbell. 2006. Controlling the false discovery rate and increasing statistical power in ecological studies. Ecoscience 13:439–442.
Wallach, A. D., W. J. Ripple, and S. P. Carroll. 2015. Novel trophic cascades: apex predators enable coexistence. Trends in Ecology and Evolution 30:146–153.
Weldon, P. J. 2004. Defensive anointing: extended chemical phenotype and unorthodox ecology. Chemoecology 14: 1–4.
Wiley, R. H. 1983. The evolution of communication: information and manipulation. Animal Behaviour 2:156–189.
Wodzicki, K. A. 1950. Introduced mammals of New Zealand. An ecological and economic survey. Department of Science and Industry, Wellington, New Zealand.
Woodley, S., A. Cloe, P. Waters, and M. J. Baum. 2004. Effects of vomeronasal organ removal on olfactory sex discrimination and odor preferences of female ferrets. Chemical Senses 29:659–669.
Wyatt, T. D. 2010. Pheromones and signature mixtures: defining species- wide signals and variable cues for identity in both invertebrates and vertebrates. Journal of Comparative Physiology 196:685–700.
Zhao, X., and D. Liu. 2015. Removal of the vomeronasal organ impairs predator odor detection in female golden hamsters. Animal Biology 65:1–12.

Supporting information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/ doi/10.1002/eap.1483/full

Data availability

Data associated with this paper have been deposited in Datastore repository http://doi.org/10.7931/J2PC308G

Appendix C

Wildlife detector dogs and camera traps: a comparison of techniques for detecting feral cats

NEW ZEALAND JOURNAL OF ZOOLOGY, 2016
VOL. 43, NO. 2, 127–137
http://dx.doi.org/10.1080/03014223.2015.1103761

Taylor & Francis
Taylor & Francis Group

RESEARCH ARTICLE

Wildlife detector dogs and camera traps: a comparison of techniques for detecting feral cats

AS Glen[a], D Anderson[b], CJ Veltman[c], PM Garvey[d] and M Nichols[e]

[a]Landcare Research, Auckland, New Zealand

[b]Landcare Research, Lincoln, New Zealand

[c]Department of Conservation, c/o Landcare Research, Palmerston North, New Zealand

[d]Centre for Biodiversity and Biosecurity, School of Biological Sciences, University of Auckland, New Zealand

[e]Centre for Wildlife Management and Conservation, Lincoln University, Canterbury, New Zealand

ARTICLE HISTORY

Received 22 May 2015

Accepted 25 September 2015

KEYWORDS carnivore; cryptic species, cats, *Felis catus*; invasive pests

ABSTRACT

A major challenge in controlling overabundant wildlife is monitoring their populations, particularly as they decline to very low density. Camera traps and wildlife detector dogs are increasingly being used for this purpose. We compared the cost-effectiveness of these two approaches for detecting feral cats (*Felis catus*) on two pastoral properties in Hawke's Bay, North Island, New Zealand. One property was subject to intensive pest removal, while the other had no recent history of pest control. Camera traps and wildlife detector dogs detected cats at similar rates at both sites. The operating costs of each method were also comparable. We identify a number of advantages and disadvantages of each technique, and suggest priorities for further research.

Introduction

Invasive predators are one of the greatest threats to global biodiversity, and their impacts in Australia and New Zealand have been catastrophic (Salo et al. 2007; Simberloff 2010). Control of invasive predators is often hindered by the difficulty of detecting them in the field; often they are cryptic, highly mobile, and occur at low density (Witmer 2005; Marks et al. 2009; Clayton & Cowan 2010). However, even very low densities of invasive predators can threaten populations of vulnerable native species (e.g. Innes et al. 2010). Camera trapping is an increasingly popular technique for monitoring cryptic carnivores (e.g. Karanth 1995; Lyra-Jorge et al. 2008; Bengsen et al. 2011a, 2011b; Brook et al. 2012; Meek et al. 2014). Wildlife detector dogs are also highly effective at communicating the presence of carnivores and/or their scats (Long et al. 2007a, 2007b; Recio et al. 2010; Brown et al. 2015).
Feral cats (Felis catus) have become widely established around the globe (Nogales et al. 2004; Campbell et al. 2011; Abbott et al. 2014), causing decline and extinction of native species, as well as detrimental impacts on humans and livestock (Medina et al. 2011, 2014; Glen et al. 2013a). To protect native prey species, cats are subject to lethal control in parts of Australia and New Zealand (Algar et al. 2007; Moseby & Hill 2011; Reardon et al. 2012). The effectiveness of control is often judged by numbers of animals removed, which provides no information on the numbers that remain (Glen et al. 2014), or by indirect measures of activity such as spotlight counts, which can suffer from low precision (Cruz et al. 2013). An affordable, accurate and precise monitoring method would better allow managers to decide where and when additional effort is needed to control feral cats. The ability to detect feral cats at very low density is also important in eradication campaigns (e.g. Campbell et al. 2011; Ramsey et al. 2011), when every last animal must be detected and/or removed. We conducted a field trial comparing the effectiveness of camera traps and wildlife detector dogs in two areas, one of which had been subject to intensive cat control. We aimed to determine: (1) whether each method could detect cats at relatively high and low abundances; and (2) which method was more cost-effective for detecting cats.

Methods

Study sites

We monitored feral cats on two pastoral properties – Waitere and Toronui Stations – in Hawke's Bay, North Island, New Zealand. Both properties are predominantly covered by introduced pasture with remnants of native vegetation. The farm landscapes include many steep gullies, which often contain thick scrub.

Waitere Station had been subject to trapping and removal of feral cats and ferrets (Mustela furo) for 3 weeks immediately before our trial commenced. A combination of leg-hold, cage and kill traps were placed throughout the property, checked daily, and captured cats and ferrets were removed. The results of the predator control will be reported in detail elsewhere; however, detections of feral cats with camera traps fell by 90% following control, suggesting that most resident cats had been

removed. Toronui Station had no recent predator control. We therefore classify Toronui Station as the high-density site and Waitere as the low-density site.

Predator monitoring

Predators were monitored using 80 camera traps for 3 weeks in May–June 2014, giving a total of 1680 camera trap-nights. The length of deployment was comparable to other camera trap surveys for feral cats (e.g. Robley et al. 2010). At each site, 40 camera traps (Reconyx Hyperfire PC900, Reconyx Inc.) were placed at approximately 500-m intervals, in a grid formation covering a total area of c. 600 ha. A high density of cameras was required for spatially explicit capture–recapture analyses as part of a parallel study. Cameras were mounted on wooden stakes with the base of the camera 10 cm above the ground. A perforated vial containing a scent lure (fresh rabbit meat) was pegged to the ground 1.5 m in front of each camera. The lure was intended to increase the likelihood of predators encountering cameras, and to encourage predators to pause in the camera's field of view so that they could be clearly photographed (Glen et al. 2013b). Because the dog survey was conducted concurrently with the camera trapping (see below), the lures were in place for both methods, and did not bias our comparison.

Cameras were set to take three photographs each time they were triggered, with no time delay between successive triggers.

Beginning on 6 June, as the camera traps were being removed, we surveyed each site using a detector dog team comprising a handler and two cat-detector dogs, which had been working with the handler for 5–7 years (Conservation Dog Team, New Zealand Department of Conservation (DOC)). In consultation with the dog handler we evaluated three possible approaches for comparing the cost-effectiveness of the camera traps and the dog team for detecting cats: (1) search within a 100-m radius of each camera trap using dogs, travelling by vehicle between search areas; (2) search along the rows of camera traps on foot, briefly circling each camera trap; (3) divide the camera trap grid into 'search cells', each containing four or more cameras, then search each cell using the dog handler's judgement to determine the optimal search pattern.

The first method was deemed unsuitable because the dogs were likely to be less effective if deployed for a series of short searches punctuated by vehicle travel; dogs cannot readily be 'switched on and off'. The second method was briefly trialled but discontinued because the dog handler judged that the fixed search pattern imposed by the grid caused likely areas of cat habitat (e.g. densely vegetated gullies) to be left unsearched. The third method was a compromise between the need to search a comparable area to that sampled by the camera traps, while operating within the practical constraints of a dog team working on foot.

Each time the dog team was deployed we used a handheld GPS to record start and finish time, path walked by the dog handler, and time and location at which the dogs detected the scent of a cat. The handler judged when cat scent had been detected based on a marked alteration in the dogs' search pattern. It was beyond the scope of this study to estimate the false-positive detection rate, therefore we assumed perfect specificity (i.e. a dog would not detect cat signs if none were present). Ideally, the

accuracy of the dog team would have been tested by genetic analysis of scats (e.g. Brown et al. 2011). However, we did not collect scat samples as our limited budget did not cover genetic analyses. The dog team continued to search a cell until either: (1) cat scent was detected, or (2) the handler judged that all likely cat habitat had been searched. We define this as a 'search event'. As our aim was simply to establish whether cats were present in a given search cell, continuing to search in a cell after cat scent had been detected would not have yielded any additional information. For cameras, we defined a search event as a 3week deployment period. For each search cell we recorded whether cats had been detected by the dogs, and/or by any of the cameras in the search cell.

Detection probabilities

We estimated the probability of detection of cats per search event using cameras and dogs (Long et al. 2007a). The detection probability of a device was conditioned on the cat population density in the area. Although the study was conducted in two areas with assumed different cat densities, both the camera and dog trials occurred under identical conditions, therefore the estimated detection probabilities were directly comparable. We used Bayesian logic and a β-binomial model (Gelman et al. 2004) to estimate the detection probability (and associated uncertainty) per search event for each method. This approach estimates distributions of detection probabilities (posteriors), avoids single-number parameter estimates (i.e. explicitly incorporates uncertainty; Clark 2005), and allows for direct comparison of methods. The approach begins with initial distributions of detection probabilities (β priors) for both methods that are based on previous studies or expert opinion (Gelman et al. 2004). The data collected in the study were then used to update the prior distributions using a binomial likelihood (hence β-binomial). In this study we used uninformed priors, (i.e. any probability between 0 and 1 was equally likely), because few previous estimates were available on detection probabilities of cats using camera traps (but see Robley et al. 2008; Robley et al. 2010; Ramsey et al. 2011).

We conducted a power analysis to determine the number of trials required to detect a range of differences in the probability of detection using detector dogs and camera traps. A sample size was deemed sufficient with power > 0.80 [P(reject $H_0|H_A$ is true)]. In this analysis the probability of detection is explicitly defined as the probability of detecting a single individual cat, given that it is present in the searched cell.

Cost estimates

We estimated the operating cost of camera trapping by recording the amount of staff time required (including time taken to review camera footage), and all associated costs such as vehicles and consumables. Costs for dogs were estimated based on daily hire rates provided by the DOC Conservation Dog Team. We compared the cost-effectiveness of camera traps and detection dogs in terms of: (1) the cost of surveying both study sites with each method, and (2) the number of search cells in which cats were detected.

Results

The camera traps and dog team detected cats at both the high-density and the low-density sites; however, poor weather forced the trial to stop before the dog team had searched both sites completely. Our comparison is therefore limited to nine search cells (five on Waitere, four on Toronui), which encompassed 41 of the 80 camera traps.

Camera traps detected cats in four of the nine search cells, whereas the dog team detected cats in five cells. There were two search cells in which cats were detected by

Table 1. Detections of cats (*Felis catus*) by camera traps and wildlife detector dogs deployed for one search event (see text for definition) in each of nine search cells on Waitere Station (low predator density) and Toronui Station (high predator density), Hawke's Bay, New Zealand.

Search cell	Site	Cameras	Dogs	Dogs' search time (minutes)
1	Waitere	0	1	14
2	Waitere	1 (1)	0	98
7	Waitere	0	0	140
8	Waitere	0	1	17
9	Waitere	0	1	17
3	Toronui	0	0	112
4	Toronui	1 (2)	1	25
5	Toronui	1 (1)	1	9
6	Toronui	1 (3)	0	109
Total		4	5	541

Note: (1 = cat detected; 0 = no cat detected). Figures in brackets indicate the number of days until cameras detected a cat in each search cell.

both methods (Table 1). Where cats were found, mean time to detection by the dogs was 16 minutes (range 13–25 minutes). In cells where cat scent was not detected, the dog team searched for an average of 109 minutes (range 76–140 minutes). On two occasions the dogs flushed a cat, providing visual confirmation that they had correctly identified the scent. We are therefore confident of the dog team's accuracy in identifying cat scent.

Detection probabilities

The posterior mean probability of detecting cats was 0.45 per search event for cameras and 0.54 per search event for dogs. The distributions of the two posterior means overlapped extensively (Figure 1), indicating no significant difference in detection probability between the two methods.

The power analysis indicated that the number of searched cells in our trial would only be sufficient to detect a very large difference (> 0.6) in detection probability between the two methods (Table 2). For simplicity we have assigned the true detection probability for cameras at 0.1 and compared this with a range of detection probabilities for dogs. However, if the true probability for cameras was closer to 0.5, the required sample sizes would be larger.

Cost estimates

Because the trial was cut short when the dog team had covered approximately half the study area, we estimated the cost of surveying the entire study area by doubling the expenses incurred by the dog team in the field. This assumes that a similar number of search cells would have been sampled each day. We estimated the operating cost to sample both study sites would be similar using wildlife detector dogs or camera traps (Table 3).

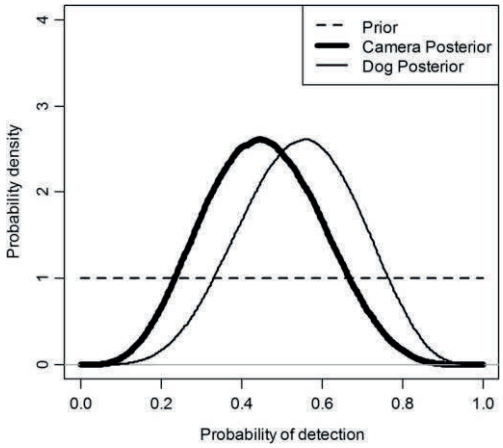


Figure 1. Estimated probability of detection for cats (Felis catus) per search event was similar using camera traps (0.45) or wildlife detector dogs (0.54). Extensive overlap between the posterior distributions indicates no significant difference in probability of detection between the two methods.

Table 2. Power analysis showing the number of search cells required to detect a difference (pDiff) in detection probability of feral cats (Felis catus) using camera traps (pCamera) and wildlife detector dogs (pDog).

pCamera	pDog	pDiff	Number of search cells
0.1	0.3	0.2	61
0.1	0.4	0.3	31
0.1	0.5	0.4	20
0.1	0.6	0.5	13
0.1	0.7	0.6	10
0.1	0.8	0.7	7
0.1	0.9	0.8	6

Table 3. Operating cost of monitoring for cats (Felis catus) on Waitere and Toronui Stations, Hawke's Bay, New Zealand, using camera traps and wildlife detector dogs.

Predator detection	Camera trapping				dogs	
	Unit price (NZD)	Number	Cost (NZD)	Number	Cost (NZD)
Batteries	1	960	960	–	–
Camera deployment and retrieval (per day)	350	8	2800	–	–
Collation of camera results (per day)	350	2	700	–	–
Vehicles (per km)	0.8	800	640	400	320
Dog team (per day)	450	–	–	10	4500
Total			5100		4820

Note: Cost estimates for dogs are extrapolated from surveys covering approximately half of each site.

Discussion

Our study suggests that the probability of detecting cats per search event was similar using either camera traps or wildlife detector dogs. Detection probabilities would be likely to vary depending on the search effort involved; therefore these estimates depend on the definition of a search event. The search effort applied in this trial was intended to represent a realistic scenario for the practical use of each method.

Although both methods detected cats in a similar number of search cells, there were only two cells in which cats were detected by both dogs and cameras. This may be a result of the different spatial and temporal scales over which these methods operate; cameras sampled at a single point over 3 weeks, whereas the dog team searched more widely within each search cell, but took a more instantaneous snapshot. It is possible that the dog team may have detected scats that were more than 3 weeks old, which may have been deposited by cats that were removed by the predator control. In this case, the estimated detection probability using wildlife detector dogs would be inflated relative to the estimate derived for camera traps. Our estimates of detection probability have wide confidence intervals, and should be regarded only as indicative. More precise estimates would require larger sample sizes than were obtained in this trial.

The estimated operating cost of each method was also comparable; however, this does not include the purchase price of the camera traps, which was NZ$56,000. Although less expensive camera traps are available, detection rates can vary substantially between different models (Meek & Pittet 2012; Meek et al. 2012; Glen et al. 2013b). We do not know whether less expensive camera traps could have achieved a comparable result.

Our cost comparison is limited to operating costs for a single survey, and does not include the cost of purchasing cameras. Ideally, depreciation of camera traps should be included; however, we have no data on the useful life of camera traps. Future research should compare the two methods for repeated surveys over a number of years. Their relative cost-effectiveness will be influenced by the

number of times cameras can be redeployed. This will depend on their durability, as well as the conditions in which they are deployed (e.g. weather conditions, likelihood of theft).

Camera traps deployed for longer than 3 weeks may have achieved a higher detection probability (e.g. Robley et al. 2010). However, the time taken for cameras to detect cats in a search cell ranged from 1 to 3 days, suggesting that 3 weeks was adequate. Although it is difficult to estimate the additional cost of deploying cameras for longer (e.g. additional analysis of footage, higher risk of camera loss/damage), it is likely these would be small compared with the costs of camera deployment and retrieval. However, a longer deployment would be less likely to satisfy assumptions of population closure.

Our estimates of detection probability using wildlife detector dogs and camera traps may help to inform the design of future studies, to estimate relative abundances of feral cats, and to assess the likelihood that eradication efforts have succeeded (e.g. Ramsey et al. 2011). To detect a significant difference in probability of detection between cameras and dogs would require a larger sample size than was achieved in this study. Therefore, although our results suggest that the methods were comparable, further trials with larger sample sizes are required. Regardless, our trial illustrated a number of advantages and disadvantages associated with camera trapping and wildlife detector dogs. The effectiveness of the dog team was dependent on fair weather as the dogs' ability to detect scent is reduced by rain or strong wind (S. Aitcheson, DOC, pers. comm.). Our cost estimates are therefore based on the assumption of 10 days of fine weather; interruptions due to bad weather would increase costs. In contrast, camera traps can operate in a wide range of weather conditions, and can be deployed for long periods so that individual weather events are less likely to influence overall results. Searching with dogs can cover an area more quickly and thoroughly than deploying camera traps at fixed positions. This may be particularly useful when rapid detection is required, e.g. a suspected incursion into a predator-free reserve. On the other hand, camera traps can operate for long periods with little or no maintenance.

Another potential advantage of wildlife detector dogs is their ability to help catch and remove animals that have survived a control programme (e.g. Ramsey et al. 2011). In contrast, camera traps are a monitoring tool only.

Camera traps may be unsuitable for use in some areas because of their vulnerability to interference by people and/or livestock. In our trial, livestock were frequently photographed by camera traps, producing many thousands of pictures and increasing the time taken to review the footage. Livestock also knocked or rubbed against cameras, sometimes leaving them inoperative. In contrast, a dog team can operate effectively in the presence of livestock. Because our trial was conducted on private property, human visitation was minimal. One camera was stolen; however, the risk of theft may be much greater in areas open to the public.

Finally, camera traps can give useful data on a wide range of other species. In the course of our trial the cameras detected numerous species of mammals and birds in addition to cats (P. Garvey

and M. Nichols, unpublished data). Although collating the data is time-consuming, such information may often be valuable to researchers or land managers.

Future research

Our study suggests that both camera traps and wildlife detector dogs may be useful for monitoring feral cats. It also draws attention to a number of questions and priorities for further research:

(1) How do detection probabilities for cats compare with those for other species? Detector dogs have been used to search for various species of carnivores (Wasser et al. 2004; Smith et al. 2005; Gompper et al. 2006; Reindl-Thompson et al. 2006; Long et al. 2007a; Dematteo et al. 2009; Brown et al. 2011) and rodents (Gsell et al. 2010; Duggan et al. 2011; Shapira et al. 2011). Detection probabilities can vary widely between species (e.g. Long et al. 2007a). However, we know of no studies that compare detection probabilities of feral cats with those of other sympatric carnivores.

(2) Is it more efficient for dogs to specialise in detecting one species, or to search for all carnivore scats, then use DNA to assign them to species? When combined with genetic analysis of scats, wildlife detector dogs can provide a fast, reliable and inexpensive way to survey for cryptic species (Long et al. 2007a). In Tasmania, trained dogs detected 80% of fox (Vulpes vulpes) scats, even after the scats had been in the field for 63 days. After 91 days in the field, 99% of fox scats were genetically identifiable to species (Brown et al. 2011; Caley et al. 2015; but see also Marks et al. 2014).

Identifying scats to species may allow population density estimates through occupancy modelling, whereas identifying individual animals allows mark–recapture analysis (Marks et al. 2009; Gleeson et al. 2010). Identifying individuals can also tell us about their movements and behaviour. However, identifying individuals from scat DNA is more expensive and requires fresher samples than identifying species. Hence, there may be a trade-off between cost and rigour of different techniques.

(1) Once the above questions have been addressed, the cost-effectiveness of detector dogs and scat DNA should be compared with other non-invasive techniques such as camera trapping.

We conclude that the choice to use camera traps or wildlife detector dogs will depend on the study aims (e.g. research versus eradication), as well as site-specific factors such as weather, land-use and degree of human visitation. Although further testing is required to compare long-term cost-effectiveness, both methods can detect feral cats at relatively high and low densities.

Acknowledgements

We are grateful to S, K and B Aitcheson, M Perry, R Dickson and S Cave for logistical support, and to B Cheetham (Landcorp, Waitere Station) and D Schaw (Toronui Station) for site access, accommodation and assistance. K Vincent

(DOC Conservation Dog Team) provided helpful advice. We thank M Barron, R Pech, G Norbury and two anonymous referees for helpful comments on a previous draft.

Associate Editor: Dr Grant Norbury.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

Funding was provided by the New Zealand Ministry for Business, Innovation and Employment, the Department of Conservation and Hawke's Bay Regional Council.

References

Abbott I, Peacock D, Short J. 2014. The new guard: the arrival and impacts of cats and foxes. In: Glen AS, Dickman CR, editors. Carnivores of Australia: past, present and future. Collingwood: CSIRO Publishing; p. 69–104.

Algar D, Angus GJ, Williams MR, Mellican AE. 2007. Influence of bait type, weather and prey abundance on bait uptake by feral cats (Felis catus) on Peron Peninsula, Western Australia. Conservation Science Western Australia. 6:109–149.

Bengsen A, Butler J, Masters P. 2011a. Estimating and indexing feral cat population abundances using camera traps. Wildlife Res. 38:732–739. doi:10.1071/WR11134.

Bengsen AJ, Leung LK-P, Lapidge SJ, Gordon IJ. 2011b. Using a general index approach to analyze camera-trap abundance indices. J Wildlife Manage. 75:1222–1227.

Brook LA, Johnson CN, Ritchie EG. 2012. Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. J Appl Ecol. 49:1278–1286. doi:10. 1111/j.1365-2664.2012.02207.x.

Brown B, Gaffney R, Pauza M, Barclay C, MacDonald A, Sarre S. 2011. The mysterious case of the disappearing poo: fox scat degradation in Tasmania. In: Saunders G, Lane C eds. Proceedings of the 15th Australasian Vertebrate Pest Conference, Australasian Vertebrate Pest Committee, Sydney, 2011; p. 161.

Brown WE, Ramsey DSL, Gaffney R. 2015. Degradation and detection of fox (Vulpes vulpes) scats in Tasmania: evidence from field trials. Wildlife Res. 41:681–690.

Caley P, Ramsey DSL, Barry SC. 2015. Inferring the distribution and demography of an invasive species from sighting data: the red fox incursion into Tasmania. PLoS ONE. 10:e0116631. doi:10.1371/journal.pone.0116631.

Campbell KJ, Harper G, Algar D, Hanson CC, Keitt BS, Robinson S. 2011. Review of feral cat eradications on islands. In: Veitch CR, Clout MN, Towns DR eds. Island Invasives: Eradication and Management. Proceedings of the International Conference on Island Invasives. Gland, Switzerland and Auckland, New Zealand, IUCN; p. 37–46.

Clark JS. 2005. Why environmental scientists are becoming Bayesians. Ecol Lett. 8:2–14. doi:10. 1111/j.1461-0248.2004.00702.x.

Clayton R, Cowan P. 2010. Management of animal and plant pests in New Zealand - patterns of control and monitoring by regional agencies. Wildlife Res. 37:360–371. doi:10.1071/WR09072.

Cruz J, Glen AS, Pech RP. 2013. Modelling landscape-level numerical responses of predators to prey: the case of cats and rabbits. PLoS ONE. 8:e73544. doi:10.1371/journal.pone.0073544.

Dematteo KE, Rinas MA, Sede MM, Davenport B, Argüelles CF, Lovett K, Parker PG. 2009. Detection dogs: an effective technique for bush dog surveys. J Wildlife Manage. 73:1436–1440. doi:10.2193/2008-545.

Duggan JM, Heske EJ, Schooley RL, Hurt A, Whitelaw A. 2011. Comparing detection dog and livetrapping surveys for a cryptic rodent. J Wildlife Manage. 75:1209–1217. doi:10.1002/jwmg.150.

Gelman A, Carlin JB, Stern HS, Rubin DB. 2004. Bayesian data analysis. Boca Raton, FL: Chapman & Hall/CRC.

Gleeson DM, Byrom A, Howitt R. 2010. Non-invasive methods for genotyping of stoats (Mustela erminea) in New Zealand: potential for field applications. New Zeal J Ecol. 34:356–359.

Glen AS, Atkinson R, Campbell KJ, Hagen E, Holmes ND, Keitt BS, Parkes JP, Saunders A, Sawyer J, Torres H. 2013a. Eradicating multiple invasive species on inhabited islands: the next big step in island restoration? Biol Invasions. 15:2589–2603.

Glen AS, Cockburn S, Nichols M, Ekanayake J, Warburton B. 2013b. Optimising camera traps for monitoring small mammals. PLoS ONE. 8:e67940. doi:10.1371/journal.pone.0067940.

Glen AS, Warburton B, Cruz J, Coleman M. 2014. Comparison of camera traps and kill traps for detecting mammalian predators: a field trial. New Zeal J Zool. 41:155–160. doi:10.1080/ 03014223.2014.898667.

Gompper ME, Kays RW, Ray JC, Lapoint SD, Bogan DA, Cryan JR. 2006. A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. Wildlife Society Bulletin. 34:1142–1151. doi:10.2193/0091-7648(2006)34[1142:ACONTT]2.0.CO;2.

Gsell A, Innes J, de Monchy P, Brunton D. 2010. The success of using trained dogs to locate sparse rodents in pest-free sanctuaries. Wildlife Res. 37:39–46. doi:10.1071/WR09117.

Innes J, Kelly D, Overton JMcC, Gillies C. 2010. Predation and other factors currently limiting New Zealand forest birds. New Zeal J Ecol. 34:86–114.

Karanth KU. 1995. Estimating tiger *Panthera tigris* populations from camera-trap data using capture-recapture models. Biol Conserv. 71:333–338.

Long RA, Donovan TM, Mackay P, Zielinski WJ, Buzas JS. 2007a. Comparing scat detection dogs, cameras, and hair snares for surveying carnivores. J Wildlife Manage. 71:2018–2025. doi:10. 2193/2006-292.

Long RA, Donovan TM, Mackay P, Zielinski WJ, Buzas JS. 2007b. Effectiveness of scat detection dogs for detecting forest carnivores. J Wildlife Manage. 71:2007–2017. doi:10.2193/2006-230.

Lyra-Jorge MC, Ciocheti G, Pivello VR, Meirelles ST. 2008. Comparing methods for sampling largeand medium-sized mammals: camera traps and track plots. Eur J Wildlife Res. 54:739–744. doi:10.1007/s10344-008-0205-8.

Marks CA, Gigliotti F, McPhee S, Piggott MP, Taylor A, Glen AS. 2009. DNA genotypes reveal red fox (Vulpes vulpes) abundance, response to lethal control and limitations of contemporary survey techniques. Wildlife Res. 36:647–658.

Marks CA, Obendorf D, Pereira F, Edwards I, Hall GP. 2014. The dispersion and detection patterns of mtDNA-assigned red fox *Vulpes vulpes* scats in Tasmania are anomalous. J Appl Ecol. 51:1033–1040.

Medina FM, Bonnaud E, Vidal E, Nogales M. 2014. Underlying impacts of invasive cats on islands: not only a question of predation. Biodivers Conserv. 23:327–342. doi:10.1007/s10531-013-0603-4.

Medina FM, Bonnaud E, Vidal E, Tershy BR, Zavaleta ES, Donlan CJ, Keitt BS, Le Corre M, Horwarth SV, Nogales M. 2011. A global review of the impacts of invasive cats on island endangered vertebrates. Global Change Biol. 17:3503–3510. doi:10.1111/j.1365-2486.2011.02464.x.

Meek P, Fleming P, Ballard G. 2012. An introduction to camera trapping for wildlife surveys in Australia. Canberra: Invasive Animals CRC.

Meek PD, Fleming PJS, Ballard G, Banks P, Claridge AW, Sanderson J, Swann D, editors. 2014. Camera trapping: wildlife research and management. Collingwood: CSIRO Publishing.

Meek PD, Pittet A. 2012. User-based design specifications for the ultimate camera trap for wildlife research. Wildlife Res. 39:649–660.

Moseby KE, Hill BM. 2011. The use of poison baits to control feral cats and red foxes in arid South Australia I: aerial baiting trials. Wildlife Res. 38:338–349. doi:10.1071/WR10235.

Nogales M, Martin A, Tershy BR, Donlan CJ, Witch D, Puerta N, Wood B, Alonso J. 2004. A review of feral cat eradication on islands. Conserv Biol. 18:310–319. doi:10.1111/j.1523-1739.2004. 00442.x.

Ramsey DSL, Parkes JP, Will D, Hanson CC, Campbell KJ. 2011. Quantifying the success of feral cat eradication, San Nicolas Island, California. New Zeal J Ecol. 35:163–173.

Reardon JT, Whitmore N, Holmes KM, Judd LM, Hutcheon AD, Norbury G, Mackenzie DI. 2012. Predator control allows critically endangered lizards to recover on mainland New Zealand. New Zeal J Ecol. 36:141–150.

Recio MR, Mathieu R, Maloney R, Seddon PJ. 2010. First results of feral cats (Felis catus) monitored with GPS collars in New Zealand. New Zeal J Ecol. 34:288–296.

Reindl-Thompson SA, Shivik JA, Whitelaw A, Hurt A, Higgins KF. 2006. Efficacy of scent dogs in detecting black-footed ferrets at a reintroduction site in South Dakota. Wildlife Society Bulletin. 34:1435–1439. doi:10.2193/0091-7648(2006)34[1435:EOSDID]2.0.CO;2.

Robley A, Gormley A, Woodford L, Lindeman M, Whitehead B, Albert R, Bowd M, Smith A. 2010. Evaluation of camera trap sampling designs used to determine change in occupancy rate and abundance of feral cats. Arthur Rylah Institute for Environmental Research Technical Report No. 201. Heidelberg, VIC: Department of Sustainability and Environment.

Robley A, Ramsey D, Woodford L, Lindeman M, Johnston M, Forsyth D. 2008. Evaluation of detection methods and sampling designs used to determine the abundance of feral cats. Heidelberg, VIC: Arthur Rylah Institute for Environmental Research, Department of Sustainability and Environment.

Salo P, Korpimäki E, Banks PB, Nordström M, Dickman CR. 2007. Alien predators are more dangerous than native predators to prey populations. Proc R Soc Lond B Biol Sci. 274:1237–1243.

Shapira I, Buchanan F, Brunton DH. 2011. Detection of caged and free-ranging Norway rats Rattus norvegicus by a rodent sniffing dog on Browns Island, Auckland, New Zealand. Conserv Evid. 8:38–42.

Simberloff D. 2010. Invasive species in New Zealand. In: Sodhi NS, Ehrlich PR, editors. Conservation biology for all. Oxford: Oxford University Press; p. 132–133.

Smith DA, Ralls K, Cypher BL, Maldonado JE. 2005. Assessment of scat-detection dog surveys to determine kit fox distribution. Wildl Soc Bull. 33:897–904. doi:10.2193/0091-7648(2005)33[897: AOSDST]2.0.CO;2.

Wasser SK, Davenport B, Ramage ER, Hunt KE, Parker M, Clarke C, Stenhouse G. 2004. Scat detection dogs in wildlife research and management: application to grizzly and black bears in the Yellowhead Ecosystem, Alberta, Canada. Can J Zool. 82:475–492. doi:10.1139/z04-020.

Witmer GW. 2005. Wildlife population monitoring: some practical considerations. Wildlife Res. 32:259–263. doi:10.1071/WR04003.

References

Abbott I 2002. Origin and spread of the cat, (*Felis catus*), on mainland Australia, with a discussion of the magnitude of its early impact on native fauna. Wildlife Research 29(1): 51-74.

Abu-Madi M, Behnke J 2014. Feline patent Toxoplasma-like coccidiosis among feral cats (Felis catus) in Doha city, Qatar and its immediate surroundings. Acta Parasitologica 59(3): 390-397.

Afonso E, Thulliez P, Gilot-Fromont E 2006. Transmission of Toxoplasma gondii in an urban population of domestic cats (Felis catus). International Journal for Parasitology 36(13): 1373-1382.

Afonso E, Thulliez P, Pontier D, Gilot-Fromont E 2007. Toxoplasmosis in prey species and consequences for prevalence in feral cats: not all prey species are equal. Parasitology 134(14): 1963-1971.

Alexander PD 2016. Comparing conventional and noninvasive monitoring techniques for assessing cougar population size in the southern Greater Yellowstone ecosystem, Utah State University.

Algar D, Burrows N 2004. Feral cat control research: Western Shield review-February 2003. Conservation Science Western Australia 5(2): 131.

Algar D, Brazell RI 2008. A bait-suspension device for the control of feral cats. Wildlife Research 35(5): 471-476.

Algar D, Angus G, Williams M, Mellican A 2007. Influence of bait type, weather and prey abundance on bait uptake by feral cats (Felis catus) on Peron Peninsula, Western Australia. Conservation Science Western Australia 6(1): 109.

Allen B, Allen L, Leung LP 2015. Interactions between two naturalised invasive predators in Australia: are feral cats suppressed by dingoes? Biological Invasions 17(2): 761-776.

Allen ML, Evans BE, Wheeler ME, Mueller MA, Pemble K, Olson ER, Van Stappen J, Van Deelen TR 2017. Survey techniques, detection probabilities, and the relative abundance of the carnivore guild on the Apostle Islands (2014-2016). arXiv preprint arXiv:1703.10726.

Alterio N, Moller H, Ratz H 1998. Movements and habitat use of feral house cats Felis catus, stoats Mustela erminea and ferrets Mustela furo, in grassland surrounding Yellow-eyed penguin Megadyptes antipodes breeding areas in spring. Biological Conservation 83(2): 187-194.

Arthur T, Gifford, E, Pech, R 1999. Tracking tunnels vs trapping in an east Australian woodland. CSIRO ed. Canberra.

Ball SJ, Ramsey D, Nugent G, Warburton B, Efford M 2005. A method for estimating wildlife detection probabilities in relation to home-range use: insights from a field study on the common brushtail possum (Trichosurus vulpecula). Wildlife Research 32(3): 217-227.

Barratt DG 1997. Home range size, habitat utilisation and movement patterns of suburban and farm cats Felis catus. Ecography 20(3): 271-280.

Bengsen A 2014. Effects of coordinated poison-baiting programs on survival and abundance in two red fox populations. Wildlife Research 41(3): 194-202.

Bengsen A, Butler J, Masters P 2011. Estimating and indexing feral cat population abundances using camera traps. Wildlife Research 38(8): 732-739.

Bengsen A, Robinson R, Chaffey C, Gavenlock J, Hornsby V, Hurst R, Fosdick M 2014. Camera trap surveys to evaluate pest animal control operations. Ecological Management & Restoration 15(1): 97-100.

Bengsen AJ, Butler JA, Masters P 2012. Applying home-range and landscape-use data to design effective feral-cat control programs. Wildlife Research 39(3): 258-265.

Berry C 1999a. Potential interactions of hedgehogs with North Island brown kiwi at Boundary Stream Mainland Island. Conservation Advisory Science Notes 268: 1-22.

Berry CJ 1999b. Potential interactions of hedgehogs with North Island brown kiwi at Boundary Stream Mainland Island. Wellington: Department of Conservation.

Bevins SN, Carver S, Boydston EE, Lyren LM, Alldredge M, Logan KA, Riley SP, Fisher RN, Vickers TW, Boyce W 2012. Three pathogens in sympatric populations of pumas, bobcats, and domestic cats: implications for infectious disease transmission. PloS one 7(2): e31403.

Biró Z, Szemethy L, Heltai M 2004. Home range sizes of wildcats (Felis silvestris) and feral domestic cats (Felis silvestris f. catus) in a hilly region of Hungary. Mammalian Biology - Zeitschrift für Säugetierkunde 69(5): 302-310.

Blackwell GL, Potter MA, McLennan JA 2002. Rodent density indices from tracking tunnels, snap-traps and Fenn traps: do they tell the same story? New Zealand Journal of Ecology 26(1): 43-52.

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24(3): 127-135.

Bonner S, Holmberg J 2013. Mark-recapture with multiple, non-invasive marks. Biometrics 69(3): 766-775.

Boonstra R, Kanter M, Krebs CJ 1992. A Tracking Technique to Locate Small Mammals at Low Densities. Journal of Mammalogy 73(3): 683-685.

Bowie M, Kavermann M, Ross J 2010. The Quail Island story-thirteen years of multi-species pest control: successes, failures and lessons learnt.

Bradshaw JW 2006. The evolutionary basis for the feeding behavior of domestic dogs (Canis familiaris) and cats (Felis catus). The Journal of Nutrition 136(7): 1927S-1931S.

Bradshaw JW, Goodwin D, Legrand-Defretin V, Nott HM 1996. Food selection by the domestic cat, an obligate carnivore. Comparative Biochemistry and Physiology Part A: Physiology 114(3): 205-209.

Brassine E, Parker D 2015. Trapping Elusive Cats: Using Intensive Camera Trapping to Estimate the Density of a Rare African Felid. PloS one 10(12): e0142508.

Brook LA, Johnson CN, Ritchie EG 2012. Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. Journal of Applied Ecology 49(6): 1278-1286.

Brown B, Gaffney, R, Pauza, M, Barclay, C, Macdonald, A, Sarre, S 2011. The mysterious case of the disappearing poo: fox scat degradation in Tasmania. . In: In: Saunders G LCe ed. Proceedings of the 15th Australasian Vertebrate Pest Conference. Pp. 161.

Brown K, Moller H, Innes J, Alterio N 1996. Calibration of tunnel tracking rates to estimate relative abundance of ship rats (*Rattus rattus*) and mice (*Mus musculus*) in a New Zealand forest. New Zealand Journal of Ecology: 271-275.

Buckland ST, Anderson DR, Burnham KP, Laake JL 2005. Distance sampling, Wiley Online Library.

Burton AC, Neilson E, Moreira D, Ladle A, Steenweg R, Fisher JT, Bayne E, Boutin S 2015. REVIEW: Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology 52(3): 675-685.

Campbell P 1973. The feeding behaviour of the hedgehog (Erinaceus europaeus L.) in pasture land in New Zealand. Proceedings (New Zealand Ecological Society). Pp. 35-40.

Can ÖE, Kandemir İ, Togan İ 2011. The wildcat Felis silvestris in northern Turkey: assessment of status using camera trapping. Oryx 45(01): 112-118.

Carbone C, Christie S, Conforti K, Coulson T, Franklin N, Ginsberg JR, Griffiths M, Holden J, Kawanishi K, Kinnaird M and others 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. Animal Conservation 4(1): 75-79.

Carvalho WD, Adania CH, Esberard CEL 2013. Comparison of two mammalian surveys made with camera traps in southeastern Brazil, focusing the abundance of wild mammals and domestic dogs/Comparacao entre duas amostragens de mamiferos feitas com armadilhas fotograficas no sudeste do Brasil, com foco na abundancia de mamiferos silvestres e caes domesticos. Brazilian Journal of Biology 73(1): 29+.

Castro-Arellano I, Madrid-Luna C, Lacher TE, LeÓN-Paniagua L 2008. Hair-Trap Efficacy for Detecting Mammalian Carnivores in the Tropics. The Journal of Wildlife Management 72(6): 1405-1412.

Caughley G 1977. Analysis of vertebrate populations. New York, Wiley.

Chandler RB, Royle JA 2013. Spatially explicit models for inference about density in unmarked or partially marked populations. The Annals of Applied Statistics 7(2): 936-954.

Chandler RB, Royle JA, King DI 2011. Inference about density and temporary emigration in unmarked populations. Ecology 92(7): 1429-1435.

Chao A 1987. Estimating the population size for capture-recapture data with unequal catchability. Biometrics: 783-791.

Chapman S, Balme G 2010. An Estimate of Leopard Population Density in a Private Reserve in KwaZulu-Natal, South Africa, using Camera—Traps and Capture-Recapture Models. South African Journal of Wildlife Research 40(2): 114-120.

Christie JE, MacKenzie DI, Greene TC, Sim JL 2015. Using passive detection devices to monitor occupancy of ship rats (Rattus rattus) in New Zealand temperate rainforest. New Zealand Journal of Ecology 39(1): 79.

Clapperton BK, Byrom, A ed. 2005. Feral ferret. *In*: King, C.M (Ed.): *The handbook of New Zealand mammals.* 2 ed. Oxford Universtiy Press, Melbourne. . 294-308 p.

Colyn RB, Radloff FGT, O'Riain MJ 2017. Camera trapping mammals in the scrubland's of the Cape Floristic Kingdom—the importance of effort, spacing and trap placement. Biodiversity and Conservation.

De Bondi N, White JG, Stevens M, Cooke R 2010. A comparison of the effectiveness of camera trapping and live trapping for sampling terrestrial small-mammal communities. Wildlife Research 37(6): 456-465.

De Milliano J, Di Stefano J, Courtney P, Temple-Smith P, Coulson G 2016. Soft-release versus hard-release for reintroduction of an endangered species: an experimental comparison using eastern barred bandicoots (*Perameles gunnii*). Wildlife Research 43(1): 1-12.

Dickman CR 1996. Overview of the impacts of feral cats on Australian native fauna, Australian Nature Conservation Agency Canberra.

Doherty TS, Bengsen AJ, Davis RA 2015. A critical review of habitat use by feral cats and key directions for future research and management. Wildlife Research 41(5): 435-446.

Domigan IR, Hughey KFD 2008. Trapping tunnel design incorporating behavioural preferences of stoats. New Zealand Journal of Zoology 35(3): 243-250.

Dorazio RM, Royle JA 2005. Estimating Size and Composition of Biological Communities by Modeling the Occurrence of Species. Journal of the American Statistical Association 100(470): 389-398.

du Preez BD, Loveridge AJ, Macdonald DW 2014. To bait or not to bait: a comparison of camera-trapping methods for estimating leopard Panthera pardus density. Biological Conservation 176: 153-161.

Dueñas JF, Cruickshank R, Ross J 2015. Optimisation of a microsatellite panel for the individual identification of brushtail possums using low template DNA. New Zealand Journal of Ecology 39(1): 93.

Eason CT, Miller A, MacMorran DB, Murphy EC 2014. Toxicology and ecotoxicology of para-aminopropiophenone (PAPP)–a new predator control tool for stoats and feral cats in New Zealand. New Zealand Journal of Ecology: 177-188.

Eason CT, Murphy E, Hix S, Henderson R, MacMorran D 2010. Susceptibility of four bird species to para-aminopropiophenone (PAPP).

Edwards G, De Preu N, Shakeshaft B, Crealy I, Paltridge R 2001. Home range and movements of male feral cats (Felis catus) in a semiarid woodland environment in central Australia. Austral Ecology 26(1): 93-101.

Edwards GP, Ealey EHM 1975. Aspects of the ecology of the swamp wallaby *Wallabia bicolor* (Marsupialia: Macropodidae). Australian Mammalogy 1: 307-317.

Edwards GP, de Preu ND, Shakeshaft BJ, Crealy IV 2000. An evaluation of two methods of assessing feral cat and dingo abundance in central Australia. Wildlife Research 27(2): 143-149.

Efford M 2004. Density estimation in live-trapping studies. Oikos 106(3): 598-610.

Efford M, Warburton B, Spencer N 2000. Home-range changes by brushtail possums in response to control. Wildlife Research 27: 117-127.

Efford MG, Warburton B, Coleman MC, Barker RJ 2005. A field test of two methods for density estimation. Wildlife Society Bulletin 33(2): 731-738.

Fancourt BA 2016. Avoiding the subject: the implications of avoidance behaviour for detecting predators. Behavioral Ecology and Sociobiology 70(9): 1535-1546.

Fisher P, Algar D, Murphy E, Johnston M, Eason C 2015. How does cat behaviour influence the development and implementation of monitoring techniques and lethal control methods for feral cats? Applied Animal Behaviour Science 173: 88-96.

Fiske I, Chandler R 2011. unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43(10): 1-23.

Forin-Wiart M-A, Gotteland C, Gilot-Fromont E, Poulle M-L 2014. Assessing the homogeneity of individual scat detection probability using the bait-marking method on a monitored free-ranging carnivore population. European Journal of Wildlife Research 60(4): 665-672.

Fryxell JM, Sinclair AR, Caughley G 2014. Wildlife ecology, conservation, and management. Oxford, John Wiley & Sons.

Garvey PM, Glen AS, Clout MN, Wyse SV, Nichols M, Pech RP 2017. Exploiting interspecific olfactory communication to monitor predators. Ecological Applications(28): 389-402.

Gerber BD, Karpanty SM, Randrianantenaina J 2012. Activity patterns of carnivores in the rain forests of Madagascar: implications for species coexistence. Journal of Mammalogy 93(3): 667-676.

Gillies C, Fitzgerald BM 2005. Feral cat. In: King, C.M (Ed.) *The handbook of New Zealand mammals*. 2 ed. Oxford University Press, Melbourne. Pp. 308-326.

Gillies CF, B.M 2005. Feral cat. In: King, C.M (Ed.) *The handbook of New Zealand mammals*. 2 ed. Oxford University Press, Melbourne. Pp. 308-326.

Glen AS, Byrom AE 2014. Implications of Landholder Buy-in for the Success of Regional-scale Predator Control: Part 1: Review of Predator Movements. Lincoln, Landcare Research.

Glen AS, Warburton B, Cruz J, Coleman M 2014. Comparison of camera traps and kill traps for detecting mammalian predators: a field trial. New Zealand Journal of Zoology 41(3): 155-160.

Glen AS, Norbury D, Garvey P, Dickson R 2017. Effectiveness of feral cat control using para-aminopropiophenon (PAPP) on Toronui Station, Hawke's Bay.

Glen AS, Cockburn S, Nichols M, Ekanayake J, Warburton B 2013. Optimising camera traps for monitoring small mammals. *PloS one* 8(6): e67940.

Glen AS, Anderson D, Veltman CJ, Garvey PM, Nichols M 2016. Wildlife detector dogs and camera traps: a comparison of techniques for detecting feral cats. New Zealand Journal of Zoology 43(2): 127-137.

Gompper ME, Kays RW, Ray JC, Lapoint SD, Bogan DA, Cryan JR 2006. A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. Wildlife Society Bulletin 34(4): 1142-1151.

Griffiths R, Buchanan F, Broome K, Neilsen J, Brown D, Weakley M 2014. Successful eradication of invasive vertebrates on Rangitoto and Motutapu Islands, New Zealand. Biological Invasions 17(5): 1355-1369.

Griffiths R, Buchanan F, Broome K, Neilsen J, Brown D, Weakley M 2015. Successful eradication of invasive vertebrates on Rangitoto and Motutapu Islands, New Zealand. Biological Invasions 17(5): 1355-1369.

Gsell A, Innes J, de Monchy P, Brunton D 2010. The success of using trained dogs to locate sparse rodents in pest-free sanctuaries. Wildlife Research 37(1): 39-46.

Guthlin D, Storch I, Kuchenhoff H 2014. Toward reliable estimates of abundance: comparing index methods to assess the abundance of a mammalian predator. PLoS ONE 9.

Hanson CC, Jolley WJ, Smith G, Garcelon DK, Keitt BS, Little AE, Campbell KJ 2015. Feral cat eradication in the presence of endemic San Nicolas Island foxes. Biological Invasions 17(4): 977-986.

Harper GA 2002. Habitat selection by feral cats (*Felis catus*) and three rat species (*Rattus* spp.) on Stewart Island (Rakiura) and their impacts on native birds. Unpublished PhD thesis, University of Otago, Dunedin.

Heilbrun RD, Silvy NJ, Tewes ME, Peterson MJ 2003. Using automatically triggered cameras to individually identify bobcats. Wildlife Society Bulletin: 748-755.

Hines JE, Nichols JD, Royle JA, MacKenzie DI, Gopalaswamy AM, Kumar NS, Karanth KU 2010. Tigers on trails: occupancy modeling for cluster sampling. Ecological Applications 20(5): 1456-1466.

Hoare JM, Adams LK, Bull LS, Towns DR 2007. Attempting to Manage Complex Predator-Prey Interactions Fails to Avert Imminent Extinction of a Threatened New Zealand Skink Population. The Journal of Wildlife Management 71(5): 1576-1584.

Hofmeester TR, Rowcliffe JM, Jansen PA 2016. A simple method for estimating the effective detection distance of camera traps. Remote Sensing in Ecology and Conservation: n/a-n/a.

Hohnen R, Ashby J, Tuft K, McGregor H 2013. Individual identification of northern quolls (Dasyurus hallucatus) using remote cameras. Australian Mammalogy 35(2): 131-135.

Jackson DB, Green RE 2000. The importance of the introduced hedgehog (Erinaceus europaeus) as a predator of the eggs of waders (Charadrii) on machair in South Uist, Scotland. Biological Conservation 93(3): 333-348.

Jackson RM, Roe JD, Wangchuk R, Hunter DO 2006. Estimating Snow Leopard Population Abundance Using Photography and Capture-Recapture Techniques. Wildlife Society Bulletin 34(3): 772-781.

Jones C, Sanders MD ed. 2005. European hedgehog. *In*: King, C.M (Ed.): *The handbook of New Zealand mammals.*
. 2 ed, Oxford University Press, Melbourne. 81-95 p.

Jones C, Moss K, Sanders M 2005. Diet of hedgehogs (Erinaceus europaeus) in the upper Waitaki Basin, New Zealand: implications for conservation. New Zealand Journal of Ecology: 29-35.

Karanth KU 1995. Estimating tiger Panthera tigris populations from camera-trap data using capture—recapture models. Biological Conservation 71(3): 333-338.

Karanth KU, Nichols JD 1998. Estimation of Tiger Densities in India Using Photographic Captures and Recaptures. Ecology 79(8): 2852-2862.

Karanth KU, Gopalaswamy AM, Kumar NS, Vaidyanathan S, Nichols JD, MacKenzie DI 2011. Monitoring carnivore populations at the landscape scale: occupancy modelling of tigers from sign surveys. Journal of Applied Ecology 48(4): 1048-1056.

Kelly MJ, Holub EL 2008. Camera Trapping of Carnivores: Trap Success among Camera Types and across Species, and Habitat Selection by Species, on Salt Pond Mountain, Giles County, Virginia. Northeastern Naturalist 15(2): 249-262.

King CM ed. 2005. Weasel. In: King, C.M (Ed.) *The handbook of New Zealand mammals*. 2 ed. Oxford University Press, Melbourne 287-308 p.

King CM, Murphy EC ed. 2005. Stoat. In: King, C.M (Ed.): *The handbook of New Zealand mammals.* 2 ed, Oxford University Press, Melbourne. 261-287 p.

King CM, Powell RA 2006. Natural History of Weasels and Stoats. Cary, GB, OUP Oxford.

King CM, McDonald RM, Martin RD, MacKenzie DI, Tempero GW, Holmes SJ 2007. Continuous monitoring of predator control operations at landscape scale. Ecological Management & Restoration 8(2): 133-139.

Krull C, Galbraith JA, Glen AS, Nathan HW 2015. Invasive vertebrates in Australia and New Zealand. In: Stow, A.; MacLean, N.; Holwell, G.I. (Editors), Austral Ark: The State of Wildilfe in Australia and New Zealand: pp 197-226. Cambridge, Cambridge University Press.

Langham N, Porter R 1991. Feral Cats (*Felis Catus*.) On New Zealand Farmland. I. Home Range. Wildlife Research 18(6): 741-760.

Lazenby BT, Mooney NJ, Dickman CR 2015a. Effects of low-level culling of feral cats in open populations: a case study from the forests of southern Tasmania. Wildlife Research 41(5): 407-420.

Lazenby BT, Mooney NJ, Dickman CR 2015b. Detecting species interactions using remote cameras: effects on small mammals of predators, conspecifics, and climate. Ecosphere 6(12): art266.

Letnic M, Greenville A, Denny E, Dickman CR, Tischler M, Gordon C, Koch F 2011. Does a top predator suppress the abundance of an invasive mesopredator at a continental scale? Global Ecology and Biogeography 20(2): 343-353.

Liberg O, Sandell M, Pontier D, Natoli E 2000. Density, spatial organisation and reproductive tactics in the domestic cat and other felids. In: Turner DC, Bateson P ed. The Domestic Cat: the Biology of its Behaviour. 2nd ed. Cambridge, UK, Cambridge University Press. Pp. 119-147.

Linden DW, Fuller AK, Royle JA, Hare MP 2017. Examining the occupancy–density relationship for a low-density carnivore. Journal of Applied Ecology: n/a-n/a.

Lofroth EC, Krebs J 2007. The abundance and distribution of wolverines in British Columbia, Canada. Journal of Wildlife Management 71(7): 2159-2169.

Long JL 2003. Introduced mammals of the world: their history, distribution and influence, Csiro Publishing.

Long RA, Donovan TM, Mackay P, Zielinski WJ, Buzas JS 2007a. Effectiveness of Scat Detection Dogs for Detecting Forest Carnivores. The Journal of Wildlife Management 71(6): 2007-2017.

Long RA, Donovan TM, Mackay P, Zielinski WJ, Buzas JS 2007b. Comparing scat detection dogs, cameras, and hair snares for surveying carnivores. The Journal of Wildlife Management 71(6): 2018-2025.

MacKenzie DI 2005. WHAT ARE THE ISSUES WITH Presence-Absence DATA FOR WILDLIFE MANAGERS? The Journal of Wildlife Management 69(3): 849-860.

Mackenzie DI, Royle JA 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42(6): 1105-1114.

MacKenzie DI, Royle JA, Brown JA, Nichols JD, Thompson W 2004. Occupancy estimation and modeling for rare and elusive populations. Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters: 149-171.

MacKenzie DI, Nichols JD, Sutton N, Kawanishi K, Bailey LL 2005. Improving inferences in population studies of rare species that are detected imperfectly. Ecology 86(5): 1101-1113.

MacKenzie DI, Nichols JD, Gideon BL, Droege S, Royle JA, Langtimm CA 2002. Estimating Site Occupancy Rates When Detection Probabilities Are Less Than One. Ecology 83(8): 2248-2255.

Macqueen P, Goldizen AW, Seddon JM 2009. Response of a southern temperate marsupial, the Tasmanian pademelon (*Thylogale billardierii*), to historical and contemporary forest fragmentation. Molecular ecology 18(15): 3291-3306.

Mann GKH, O'Riain MJ, Parker DM 2015. The road less travelled: assessing variation in mammal detection probabilities with camera traps in a semi-arid biodiversity hotspot. Biodiversity and Conservation 24(3): 531-545.

McGregor H, Legge S, Jones ME, Johnson CN 2015. Feral cats are better killers in open habitats, revealed by animal-borne video. PloS one 10(8): e0133915.

McGregor HW, Hampton JO, Lisle D, Legge S 2016. Live-capture of feral cats using tracking dogs and darting, with comparisons to leg-hold trapping. Wildlife Research 43(4): 313-322.

McLennan J, Potter M, Robertson H, Wake G, Colbourne R, Dew L, Joyce L, McCann A, Miles J, Miller P 1996. Role of predation in the decline of kiwi, Apteryx spp., in New Zealand. New Zealand Journal of Ecology 20(1): 27-35.

Medina FM, Bonnaud E, Vidal E, Nogales M 2014. Underlying impacts of invasive cats on islands: not only a question of predation. Biodiversity and Conservation 23(2): 327-342.

Medina FM, Bonnaud E, Vidal E, Tershy BR, Zavaleta ES, Josh Donlan C, Keitt BS, Le Corre M, Horwath SV, Nogales M 2011. A global review of the impacts of invasive cats on island endangered vertebrates. Global Change Biology 17(11): 3503-3510.

Meek P, Ballard G, Fleming P 2012. An introduction to camera trapping for wildlife surveys in Australia. Canberra: Invasive Animals CRC.

Meek P, Jenkins D, Morris B, Ardler A, Hawksby R 1995. Use of two humane leg-hold traps for catching pest species. Wildlife Research 22(6): 733-739.

Meek P, Ballard G, Claridge A, Kays R, Moseby K, O'Brien T, O'Connell A, Sanderson J, Swann D, Tobler M 2014a. Recommended guiding principles for reporting on camera trapping research. Biodiversity and Conservation 23(9): 2321-2343.

Meek P, Ballard G, Claridge A, Kays R, Moseby K, O'Brien T, O'Connell A, Sanderson J, Swann D, Tobler M 2014b. Recommended guiding principles for reporting on camera trapping research. Biodiversity and Conservation: 1-23.

Meek PD, Ballard G-A, Fleming PJ 2015. The pitfalls of wildlife camera trapping as a survey tool in Australia. Australian Mammalogy 37(1): 13-22.

Moller H, Alterio N 1999. Home range and spatial organisation of stoats (Mustela erminea), ferrets (Mustela furo) and feral house cats (Felis catus) on coastal grasslands, Otago Peninsula, New Zealand: Implications for yellow-eyed penguin (Megadyptes antipodes) conservation. New Zealand Journal of Zoology 26(3): 165-174.

Moseby KE, Hill BM 2011. The use of poison baits to control feral cats and red foxes in arid South Australia I. Aerial baiting trials. Wildlife Research 38(4): 338-349.

Murphy E, Shapiro L, Hix S, MacMorran D, Eason CT 2011. Control and eradication of feral cats: field trials of a new toxin.

Murphy EC 1996. Ferrets as threats to conservation values. Royal Society of NZ, Miscellaneous Series 36: 48-51.

Murphy EC, Keedwell RJ, Brown KP, Westbrooke I 2004. Diet of mammalian predators in braided river beds in the central South Island, New Zealand. Wildlife Research 31(6): 631-638.

Nakagawa S, Schielzeth H 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4(2): 133-142.

Nichols M, Glen AS, Garvey P, Ross J 2017a. A comparison of horizontal versus vertical camera placement to detect feral cats and mustelids. New Zealand Journal of Ecology 41(1): 145-150.

Nichols M, Glen AS, Ross J, Garvey PM 2017b. A comparison of statistical modelling methods for evaluating the effectiveness of a feral cat control operation using camera traps. Unpublished manuscript.

Nogales M, Vidal E, Medina FM, Bonnaud E, Tershy BR, Campbell KJ, Zavaleta ES 2013. Feral cats and biodiversity conservation: the urgent prioritization of island management. BioScience 63(10): 804-810.

Nogales M, MartÍN A, Tershy BR, Donlan CJ, Veitch D, Puerta N, Wood B, Alonso J 2004. A Review of Feral Cat Eradication on Islands

Revisión de la Erradicación de Gatos Asilvestrados en Islas. Conservation Biology 18(2): 310-319.

Norton MA, Claridge AW, French K, Prentice A 2011. Population biology of the long-nosed potoroo (*Potorous tridactylus*) in the Southern Highlands of New South Wales. Australian Journal of Zoology 58(6): 362-368.

O'Connell AF, Bailey LL 2011. Inference for Occupancy and Occupancy Dynamics. In: O'Connell AF, Nichols JD, Karanth KU ed. Camera Traps in Animal Ecology: Methods and Analyses. Tokyo, Springer Japan. Pp. 191-204.

Olifiers N, Loretto D, Rademaker V, Cerqueira R 2011. Comparing the effectiveness of tracking methods for medium to large-sized mammals of Pantanal. Zoologia (Curitiba) 28: 207-213.

Oppel S, Burns F, Vickery J, George K, Ellick G, Leo D, Hillman JC 2014. Habitat-specific effectiveness of feral cat control for the conservation of an endemic ground-nesting bird species. Journal of Applied Ecology 51(5): 1246-1254.

Otis DL, Burnham KP, White GC, Anderson DR 1978. Statistical inference from capture data on closed animal populations. Wildlife monographs(62): 3-135.

Parkes J 1975. Some aspects of the biology of the hedgehog (Erinaceus europaeus L.) in the Manawatu, New Zealand. New Zealand Journal of Zoology 2(4): 463-472.

Parkes J, Fisher P, Robinson S, Aguirre-Muñoz A 2014. Eradication of feral cats from large islands: an assessment of the effort required for success. New Zealand Journal of Ecology: 307-314.

Paull DJ, Claridge AW, Cunningham RB 2012. Effective detection methods for medium-sized ground-dwelling mammals: a comparison between infrared digital cameras and hair tunnels. Wildlife Research 39(6): 546-553.

Pebsworth PA, LaFleur M 2014. Advancing primate research and conservation through the use of camera traps: introduction to the special issue. International Journal of Primatology 35(5): 825-840.

Pickerell GA, O'Donnell CF, Wilson DJ, Seddon PJ 2014. How can we detect introduced mammalian predators in non-forest habitats? A comparison of techniques. New Zealand Journal of Ecology 38(1): 86-102.

Plummer M 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd international workshop on distributed statistical computing. Pp. 125.

Pollock KH, Nichols JD, Brownie C, Hines JE 1990. Statistical Inference for Capture-Recapture Experiments. Wildlife Monographs(107): 3-97.

Pollock KH, Nichols JD, Simons TR, Farnsworth GL, Bailey LL, Sauer JR 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. Environmetrics 13(2): 105-119.

Quinn GP, Keough MJ 2002. Experimental design and data analysis for biologists, Cambridge University Press.

R Development Core Team 2016. R: A language and environment for statistical computing. Vienna, Austria. http://www.R-project.org/.

Ramsey D, Efford M, Ball S, Nugent G 2005. The evaluation of indices of animal abundance using spatial simulation of animal trapping. Wildlife Research 32(3): 229-237.

Ramsey DS, Parkes JP, Will D, Hanson CC, Campbell KJ 2011. Quantifying the success of feral cat eradication, San Nicolas Island, California. New Zealand Journal of Ecology: 163-173.

Ramsey DSL, Caley PA, Robley A 2015. Estimating population density from presence–absence data using a spatially explicit model. The Journal of Wildlife Management 79(3): 491-499.

Reardon JT, Whitmore N, Holmes KM, Judd LM, Hutcheon AD, Norbury G, Mackenzie DI 2012. Predator control allows critically endangered lizards to recover on mainland New Zealand. New Zealand Journal of Ecology: 141-150.

Recio M, Seddon P 2013. Understanding determinants of home range behaviour of feral cats as introduced apex predators in insular ecosystems: a spatial approach. Behavioral Ecology and Sociobiology 67(12): 1971-1981.

Recio MR 2016. Crowded house: nest sharing among solitary European hedgehogs in New Zealand. Frontiers in Ecology and the Environment 14(4): 225-226.

Recio MR, Mathieu R, Seddon PJ 2011. Design of a GPS backpack to track European hedgehogs Erinaceus europaeus. European Journal of Wildlife Research 57(6): 1175-1178.

Reed SE, Bidlack AL, Hurt A, Getz WM 2011. Detection distance and environmental factors in conservation detection dog surveys. The Journal of Wildlife Management 75(1): 243-251.

Rich LN, Davis CL, Farris ZJ, Miller DA, Tucker JM, Hamel S, Farhadinia MS, Steenweg R, Di Bitetti MS, Thapa K 2017. Assessing global patterns in mammalian carnivore occupancy and richness by integrating local camera trap surveys. Global Ecology and Biogeography 26(8): 918-929.

Robley A, Gormley AM, Forsyth DM, Triggs B 2014. Long-term and large-scale control of the introduced red fox increases native mammal occupancy in Australian forests. Biological Conservation 180: 262-269.

Robley A, Gormley A, Woodford L, Lindeman M, Whitehead B, Albert R, Bowd M, Smith A 2010. Evaluation of camera trap sampling designs used to determine change in occupancy rate and abundance of feral cats. (Arthur Rylah Institute for Environmental Research Technical Report: Melbourne.)(201).

Rowcliffe JM, Carbone C 2008. Surveys using camera traps: are we looking to a brighter future? Animal Conservation 11(3): 185-186.

Royle JA 2006. Site Occupancy Models with Heterogeneous Detection Probabilities. Biometrics 62(1): 97-102.

Royle JA, Nichols JD 2003. Estimating Abundance from Repeated Presence-Absence Data or Point Counts. Ecology 84(3): 777-790.

Royle JA, Young KV 2008. A HIERARCHICAL MODEL FOR SPATIAL CAPTURE–RECAPTURE DATA. Ecology 89(8): 2281-2289.

Royle JA, Dorazio RM 2009. 5 - INFERENCE IN CLOSED POPULATIONS. Hierarchical Modeling and Inference in Ecology. San Diego, Academic Press. Pp. 159-190.

Royle JA, Chandler RB, Gazenski KD, Graves TA 2013. Spatial capture–recapture models for jointly estimating population density and landscape connectivity. Ecology 94(2): 287-294.

Russell JC, Hasler N, Klette R, Rosenhahn B 2009. Automatic track recognition of footprints for identifying cryptic species. Ecology 90(7): 2007-2013.

Russell RE, Royle JA, Desimone R, Schwartz MK, Edwards VL, Pilgrim KP, Mckelvey KS 2012. Estimating abundance of mountain lions from unstructured spatial sampling. The Journal of Wildlife Management 76(8): 1551-1561.

Sam S 2011. New Monitoring and Control Tools for Simultaneously Managing Possums, Rats and Mice in New Zealand. Unpublished thesis, Lincoln University. 149 p.

Sarmento P, Cruz J, Eira C, Fonseca C 2009. Evaluation of Camera Trapping for Estimating Red Fox Abundance. The Journal of Wildlife Management 73(7): 1207-1212.

Shanahan DF, Mathieu R, Seddon PJ 2007. Fine-scale movement of the European hedgehog: an application of spool-and-thread tracking. New Zealand Journal of Ecology: 160-168.

Silveira L, Jácomo ATA, Diniz-Filho JAF 2003. Camera trap, line transect census and track surveys: a comparative evaluation. Biological Conservation 114(3): 351-355.

Smith JK, Coulson G 2012. A comparison of vertical and horizontal camera trap orientations for detection of potoroos and bandicoots. Australian Mammalogy 34(2): 196-201.

Sorensen A, Milligan S, Larsen T, Graham K, Eiken HG, Hagen S, Aarne SG, Fløystad IMB, Stenhouse G 2017. Using scat DNA and citizen science to determine grizzly bear distribution and abundance in West-Central, Alberta.

Stanley TR, Royle JA 2005. Estimating site occupancy and abundance using indirect detection indices. Journal of Wildlife Management 69(3): 874-883.

Stokeld D, Frank ASK, Hill B, Choy JL, Mahney T, Stevens A, Young S, Rangers D, Rangers W, Gillespie GR 2016. Multiple cameras required to reliably detect feral cats in northern Australian tropical savanna: an evaluation of sampling design when using camera traps. Wildlife Research 42(8): 642-649.

Swann DE, Hass CC, Dalton DC, Wolf SA 2004. Infrared-triggered cameras for detecting wildlife: an evaluation and review. Wildlife Society Bulletin 32(2): 357-365.

Sweetapple P, Nugent G 2011. Chew-track-cards: a multiple-species small mammal detection device. New Zealand Journal of Ecology 35(2): 153.

Taylor BD, Goldingay RL, Lindsay JM 2013. Horizontal or vertical? Camera trap orientations and recording modes for detecting potoroos, bandicoots and pademelons. *Australian Mammalogy* 36: 60-66.

Tobler MW, Zúñiga Hartley A, Carrillo-Percastegui SE, Powell GV 2015. Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. Journal of Applied Ecology 52(2): 413-421.

Tompkins DM, Byrom AE, Pech RP 2013. Predicted responses of invasive mammal communities to climate-related changes in mast frequency in forest ecosystems. Ecological Applications 23(5): 1075-1085.

Trewby ID, Young R, McDonald RA, Wilson GJ, Davison J, Walker N, Robertson A, Doncaster CP, Delahay RJ 2014. Impacts of removing badgers on localised counts of hedgehogs. PloS one 9(4): e95477.

Turner DC, Bateson P ed. 2000. The Domestic Cat: the Biology of its Behaviour. Cambridge, UK, Cambridge University Press.

Wang SW, Macdonald DW 2009. The use of camera traps for estimating tiger and leopard populations in the high altitude mountains of Bhutan. Biological Conservation 142(3): 606-613.

Warburton B, Poutu N 2002. Effectiveness of three trapping systems for killing feral cats, Department of Conservation.

Watts CH, Armstrong DP, Innes J, Thornburrow D 2011. Dramatic increases in weta (Orthoptera) following mammal eradication on Maungatautari – evidence from pitfalls and tracking tunnels. New Zealand Journal of Ecology 35(3): 261-272.

White GC, Burnham KP 1999. Program MARK: survival estimation from populations of marked animals. Bird study 46(sup1): S120-S139.

Young R, Davison J, Trewby I, Wilson G, Delahay R, Doncaster C 2006. Abundance of hedgehogs (Erinaceus europaeus) in relation to the density and distribution of badgers (Meles meles). Journal of Zoology 269(3): 349-356.

Zielinski WJ, Schlexer FV, Pilgrim KL, Schwartz MK 2006. The Efficacy of Wire and Glue Hair Snares in Identifying Mesocarnivores. Wildlife Society Bulletin 34(4): 1152-1161.